

HIGHER TAXONOMIC
CATEGORIES OF
GEKKONID LIZARDS
AND THEIR EVOLUTION

ARNOLD G. KLUGE

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 135 : ARTICLE 1 NEW YORK : 1967

HIGHER TAXONOMIC CATEGORIES OF
GEKKONID LIZARDS AND
THEIR EVOLUTION

ARNOLD G. KLUGE

*Assistant Professor of Zoology
The University of Michigan
Ann Arbor, Michigan*

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 135 : ARTICLE 1 NEW YORK : 1967

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 135, article 1, pages 1-60, text figures 1-8,
plates 1-5, tables 1-3, maps 1, 2

Issued January 20, 1967

Price: \$2.50 a copy

CONTENTS

INTRODUCTION	5
Acknowledgments	8
Methods and Materials	9
THE FAMILY GEKKONIDAE	10
Family Gekkonidae	10
Characterization	10
Range	12
Fossil History	12
THE SUBFAMILIAL CLASSIFICATION	14
Shape of the Pupil as a Systematic Character	14
Analysis of Characters	14
True Eyelids or Spectacle	15
Premaxillary Bone	15
Endolymphatic Apparatus	16
Preanal Organs and Escutcheon Scales	17
Ability to Vocalize	18
Number of Eggs Laid	19
Supratemporal Bone	19
Number of Scleral Ossicles	20
Cloacal Sacs and Bones	24
Angular Bone	33
Splénial Bone	33
Frontal Bone	33
Nasal Bones	34
Parietal Bone	35
Amphicoelous or Procoelous Presacral Vertebrae	35
Hyoid Arch	36
Second Visceral Arch	38
Squamosal Bone	38
Evolution of the Subfamilies	39
Subfamily Eublepharinae	41
Subfamily Diplodactylinae	41
Subfamily Gekkoninae	42
Subfamily Sphaerodactylinae	42
Zoogeographical History of the Subfamilies	44
SUMMARY	51
APPENDIX 1	53
LITERATURE CITED	55

INTRODUCTION

THE FAMILY GEKKONIDAE comprises a well-circumscribed, natural group of lizards, consisting of 82 genera and more than 650 species and an additional 175 subspecies. The family is widely distributed between latitude 50° N. and latitude 50° S. (map 1). Gekkos are found on all major land masses and have been successful in invading most oceanic islands. They have become adapted to the rainless northern coast of Chile and to the extreme monsoon region of eastern India.

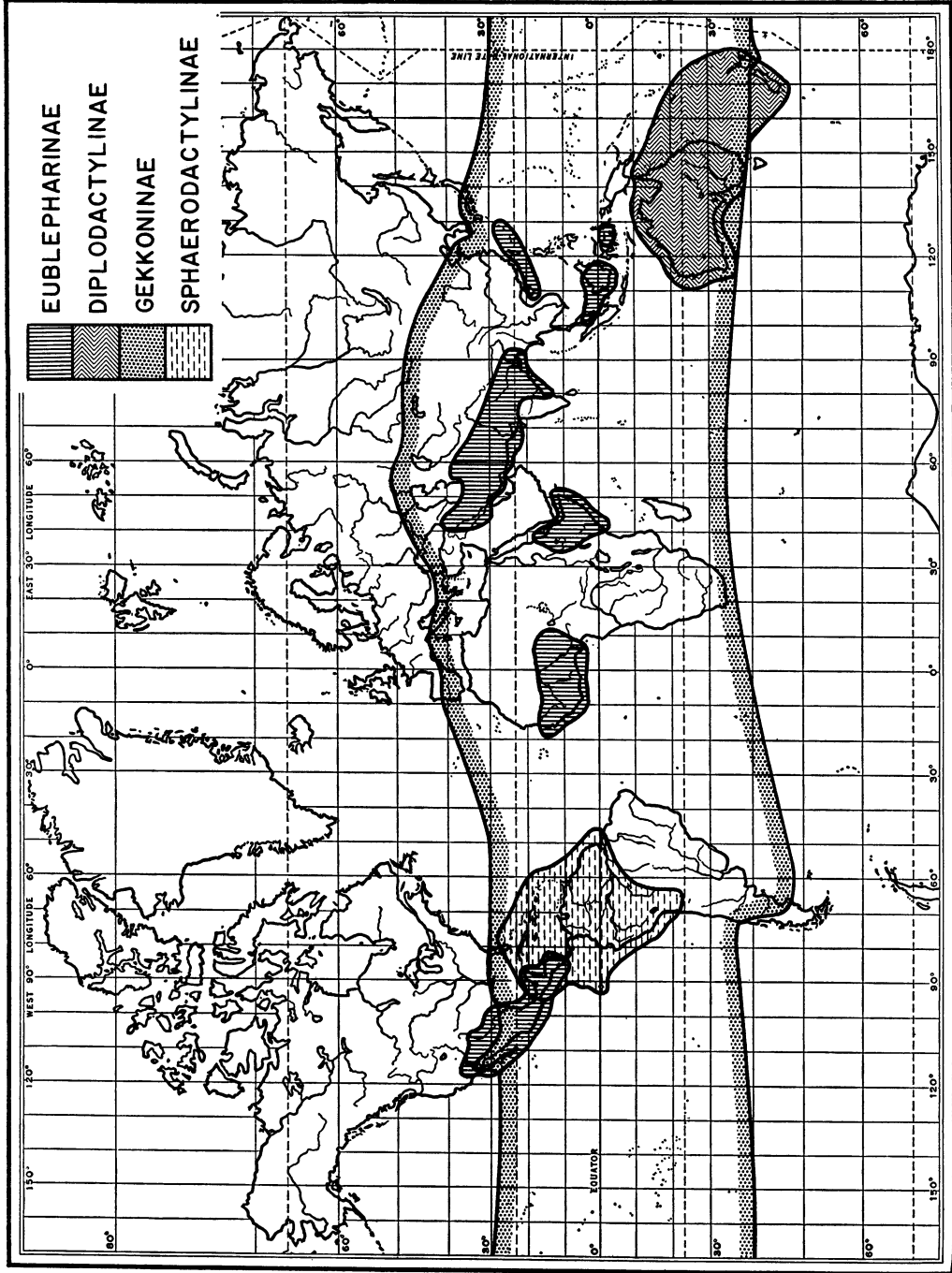
Within the family Gekkonidae there is a vast array of structural and biological diversity. Adults vary from less than 40 mm. to considerably more than 350 mm. in total length. Usually the body is flattened, but some species are compressed and approach the habitus of true chameleons. A few forms have extensive skin folds on the body and tail which, when extended, enable the animal to glide from tree to tree; some species have large dorsal crests on the body and tail. The scalation may be either homogeneous or heterogeneous and consists of minute granules, tubercles, or large platelike scales that range from being juxtaposed to being imbricate. Scale sensory organs are common. Most gekkos have a thin, delicate skin which is loosely attached by connective tissue to the underlying muscles or bone. Some species have very thick skins supplied with osteoderms which may or may not be fused to part or to all of the skull.

Gekkonid lizards are well known for their extremely variable digits and tails and their ability to vocalize. The digits are long and slender, angulate or straight to extremely dilated. The hands and feet may be fully webbed, and the claws may be retractable into specialized sheaths. The fifth digit, and claws numbering from one to four, may be lost. The dilated areas or "pads" consist of narrow to wide, divided or undivided lamellae, each of which bears numerous microscopic, hooklike projections that appear to facilitate movement in the arboreal environment by catching on surface irregularities; also, the existence of a climbing mechanism dependent on an electrostatic charge has recently been repostulated by Maderson

(1964). The tails of gekkonid lizards, which are almost always autotomic, vary from being long and attenuate or depressed (leaflike) to being extremely short and bulbous. Some tails have a subepidermal lymphatic ejecting mechanism (Bustard, 1964), and a few others are prehensile. The distal under surface of the tail, when prehensile, is in many cases covered with lamellae, similar in structure to those of the digits. The tail apparently serves as a food reservoir in those cases in which it becomes extremely swollen with fatty tissue.

Most gekkos vocalize. The sounds produced are extremely variable in pitch, duration, and frequency. The call may vary from isolated clicks to a trilled series of chirps, deep-throated barks, or quacking ducklike sounds. Some species are reported to call in large choruses with an "almost deafening" volume (Loveridge, 1947; see also Brain, 1962a). There is evidence in a few cases that the calls of closely related species are different (Haacke, 1964; Werner, 1965). The vocalizations appear to aid in the establishing of territories (Mertens, 1955; Werner, 1965), and it has been suggested that they may also discourage predators. In the genus *Teratoscincus*, each species rubs together its greatly enlarged supracaudal plates to produce a shrill, cricket-like noise (Gadow, 1901; Mertens, 1946).

In the few species of gekkos that have been studied, the reproductive behavior is complex. It may involve various precopulatory movements of the body, head, and tail, vocalizations, the contact of preanal pores and cloacal sacs, and the use of cloacal bones to enlarge the cloacal aperture which facilitates the introduction of one of the hemipenes (Greenberg, 1943). Some species exhibit no definite seasonal reproductive cycle, and mating may take place throughout the year, but in other forms breeding appears to be cyclic and restricted to a very short period during the year. There is evidence that some females can retain sperm for a considerable period (Church, 1962; Quesnel, 1957). In others, delayed oviposition occurs until embryonic development is well advanced. Most species of gekkos lay one or



MAP 1. Present distribution of the family Gekkonidae and the subfamilies Eublepharinae, Diplodactylinae, Gekkoninae, and Sphaerodactylinae as they are defined in this study.

two uniformly white, round to oval, calcareous-shelled eggs. A few species bear living young, in which case a shell-secreting area in the oviducts is absent (McCann, 1955); in these species the newborn young are from one-third to one-half of the size of the parent. The eggshell is soft, pliable, and moist when first laid but hardens and dries after a short exposure to air. Some eggs have an adhesive glutinous covering when laid which enables them to adhere to one another and to vertical surfaces. A fertile egg may measure as much as 17 mm. in length and 21 mm. in diameter. Eggs of some species can withstand long periods of exposure to sea water (11 days and probably longer) and still remain viable (Brown and Alcalá, 1957). The incubation period of the eggs varies from 40 to longer than 70 days (122 days has been reported; Kopstein, 1938), and, upon hatching, the young gekko invariably sheds its skin and often eats it. Communal egg laying appears to be common; 186 eggs were collected from one window-shutter (Mell, 1922). Gekkos apparently do not guard their eggs nor do they exhibit any paternal care of the young. Sexual maturity may be attained within 30 to 40 days (Cagle, 1946). Adults shed their skin in flakes or very large pieces at least twice a year.

Gekkonid lizards may be solitary or gregarious (20 of one form were collected under a small strip of bark, and 31 of another inside a basaltic boulder; Oliver and Shaw, 1953, and Hoofien, 1962), and a few species are commonly found in association with man. Gekkos are terrestrial, arboreal, or both, and some are known to enter fresh water (Annandale, 1905); a few are cavernicolous (Inger and King, 1961; Kluge, 1963). One species has an altitudinal distribution from near sea level (500 meters) to 4000 meters (Bons, 1959). Gekkonids spend their inactive periods under rocks, bark, natural debris, or refuse of human habitation. Some species of gekkos occupy vacated burrows of other organisms such as spiders, lizards, and mammals, whereas others excavate their own tunnels which vary from being horizontal to being nearly vertical relative to the surface of the ground. Self-excavated burrows have been found to extend more than 16 inches below the surface of the ground and may reach $2\frac{1}{2}$ to

3 feet in length. The burrow may be simple in structure or consist of a major tunnel with many blind side branches which approach the surface of the ground (Haacke, 1964). Most gekkos are nocturnal, but some species actively feed and bask in direct sunlight; many are active during the day but do not move beyond shade. Some nocturnal species are occasionally, but apparently not fortuitously, active in the sunlight (Brattstrom, 1965; Werner, 1965). Peritoneal and cranial pigmentation has been noted in a few supposedly nocturnal species. The body temperatures of active nocturnal gekkos have been reported from 10.2° C. to as high as 34.0° C. (mean ranges, 15.2° C. to 27.6° C.) and for a diurnal species from 28.5° C. to 36.5° C. (mean, 32.7° C.). The critical thermal maximum for nocturnal animals has been shown to range from 41.6° C. to 45.5° C. and for a diurnal species from 43.5° C. to 44.4° C. Nocturnal gekkos attempt to reduce their body temperatures by panting earlier than their diurnal counterparts (panting starts in nocturnal species at temperatures from 31.0° C. to 39.7° C. and in a diurnal species from 41.4° C. to 42.5° C.). Gekkos also commonly respond to excessive heat by attempting to burrow into the ground or by standing with their legs straightened so that the body and tail are elevated above the substrate (Brain, 1962b; Brattstrom, 1965; Stebbins, 1961).

The margins of the iris are extremely mobile, and apparently this mobility has enabled members of the family to adapt to a wide range of light intensities (Werner, 1965). The pupil area can be changed as much as 300-fold (Denton, 1956); this degree of mobility enables the animal to shield the pure rod retina from saturating light. The two irises are completely independent of each other and are under voluntary control (Denton, 1956). "Eyeshine" has been detected in some nocturnal gekkos. In most forms the eyes are protected by a spectacle (brille) instead of movable (true) eyelids. It is common for gekkos to lick the spectacle with their tongues and apparently clean its surface in absence of movable eyelids which normally perform this function (Bustard, 1963; Werner 1965).

Gekkonids are usually various shades of

gray or brown. These colors seem to be associated with their predominantly nocturnal habits. Diurnal species may be yellow, red, blue, or bright green. Intrasexual and intersexual dichromatism is moderately rare. Metachrosis is pronounced in a few diurnal forms. The oral cavity and tongue may be white, pink, blue, or black.

Most gekkos feed on arthropods (primarily insects), but the larger species eat other lizards and even small birds and mammals, including bats. Some species have been reported to eat snails, tidal crustaceans, and the fruits, bark exudate, and flowers of plants (McCann, 1955). Common predators on gekkos include mammals, birds, snakes, lizards, and a wide variety of arthropods (spiders and centipeds). The Gekkonidae exhibit diploid chromosome numbers of 32 to 46; metacentric chromosomes (4) have been described in one species (Goin and Goin 1962; Werner, 1956).

All the major families of lizards, with the exception of the Gekkonidae (and possibly the Scincidae), have proved to be stable taxonomic units since the nineteenth century (Underwood, 1954). Efforts to classify gekkos largely on the basis of the form of the digit (Boulenger, 1885) and the shape of the pupil (Underwood, 1954) have proved to be inadequate for delimiting natural assemblages of genera (Stephenson, 1960; Kluge, 1964). The present research is a further attempt to define the major evolutionary lines within the family Gekkonidae, but on the basis of multiple external and internal characters. The degree of relationship between the lines and the nature, direction, and amount of evolutionary change that each assemblage has undergone are also considered.

The affinities of the Gekkonidae are first briefly discussed and then followed by a detailed characterization of the family. The fossil history of the family and related groups is reviewed in an effort to determine the age of the assemblage and the relative primitiveness of the characters used in the study. The characters that appear to be significant in a definition of the major evolutionary lines within the Gekkonidae are then discussed in detail preceding the section on coding, weighting, and character associations. From an analysis of the character associations I have defined four major groups

of genera within the family: the Eublepharinae, Diplodactylinae, Gekkoninae, and Sphaerodactylinae. The number of assemblages recognized, and their names, coincide with those of previous studies. It is important to note, however, that the subfamilial names Gekkoninae and Diplodactylinae are retained, even though they differ markedly from those of Underwood (1954) in their generic composition. Also, the eublepharine and sphaerodactylinae groups are considered to be of a taxonomic rank equal to that of the Gekkoninae and the Diplodactylinae, in contrast to Underwood's arrangement in which they are treated as families. Finally, a general evolutionary and zoogeographical history of the subfamilies is postulated. For simplicity's sake, particularly in the section on the analysis of characters, I have used the names of the subfamilies that are defined later in the study rather than repeat the numerous generic names for each character-state under discussion.

ACKNOWLEDGMENTS

During the last six years many people and institutions throughout the world have contributed valuable material, information, and advice to the present study. The successful completion of this research could not have been realized without their aid. It is with pleasure that I thank Mr. Kraig K. Adler, Mr. Jerry A. Anderson, Mr. Richard E. Barwick, Dr. Charles M. Bogert, Mr. Stanley Breeden, Mr. John H. Calaby, Mr. Harold G. Cogger, Mr. James D. Fawcett, Dr. Vivian F. FitzSimons, Mr. Dale L. Hoyt, Dr. Robert F. Inger, Dr. A. K. Lee, Mr. Hymen Marx, Dr. Sherman A. Minton, Jr., Mr. F. J. Mitchell, Dr. Georges Pasteur, Dr. Glen M. Storr, Dr. Charles F. Walker, and Dr. Richard G. Zweifel. I wish to express my gratitude to Dr. A. R. Main of the Department of Zoology, University of Western Australia, who was largely responsible for the success of my study program in Australia from July, 1961, to September, 1962, where much of the present research was carried out.

I wish to thank Dr. Garth L. Underwood of the Faculty of Agriculture, University of the West Indies, Trinidad, for introducing me to the major classification of gekkos and offering many valuable suggestions. I am greatly indebted to Dr. Ernest E. Williams of the

Museum of Comparative Zoology, Harvard University, for his counseling, suggestions, and criticisms during the course of this study. Dr. Williams made available to me many critical species of gekkonids; the completeness of the generic survey is due principally to his generosity. Dr. Jay M. Savage of the Department of Biology, University of Southern California, is responsible for my interest in the evolution and zoogeography of gekkonid lizards. Under his guidance all my graduate studies were carried out, and to him I extend my sincere appreciation.

The present study was aided in part by the National Institutes of Health, Institute of Arthritis and Metabolic Diseases, Grant A-3549. I thank the Department of State, Office of Educational Exchange, Washington, D. C., which made possible the granting of a Fulbright Scholarship to Australia and the Intra-Australian Travel Award from July, 1961, to September, 1962. Sigma Xi and R.E.S.A. Societies provided financial assistance during the summer of 1963, so that I was able to study gekkonid material in the collections of museums in the United States.

METHODS AND MATERIALS

In the present study I have examined the soft parts and skeleton of examples of 74 genera and 195 species and subspecies, represented by 548 whole specimens (see Appendix 1). An additional eight genera and 88 species were examined to obtain further information on scleral ossicle numbers and the condition of the nasal and parietal bones (those listed in table 1 but not in Appendix 1). The specimens used in the osteological analyses were prepared either by the clearing and staining (Alizarin red-S) technique outlined by Davis and Gore (1947) or by the use of dermestid beetles. Additional skeletal information was obtained from stereoscopic radiographs with the use of low- and high-voltage X rays. All observations were made through low-power objectives of a stereoscopic dissecting microscope, and detailed dissection of the soft anatomy and disarticulation of the skeleton were carried out when necessary. Osteological terminology follows Romer (1956) and Kluge (1962) unless otherwise stated.

It has not been possible within the limits of this study to determine the validity of

every genus and species from which information was taken. As a matter of convenience I have selected the recent check list of the gekkos of the world by Wermuth (1965) as the authority on recognized genera and species and the spellings of scientific names. Only in the cases of *Alsophylax tuberculatus* (= *Bunopus tuberculatus*), *Gekko listeri* (= *Lepidodactylus listeri*), *Gekko oorti* (= *Lepidodactylus oorti*), *Gekko pumilus* (= *Lepidodactylus pumilus*), *Gekko smaragdinus* (= *Pseudogekko smaragdinus*), *Gymnodactylus antillensis* (= *Gonatodes antillensis*), *Pseudogekko shebae* (= *Lepidodactylus shebae*), and *Tropicolotes helenae* (= *Microgekko helenae*) have I used new combinations without here giving justification. My evidence supporting these changes is in preparation. Also, I have recognized the following: *Aelurosscalabotes dorsalis* as a species distinct from *A. felinus* (Kluge, in preparation); *Coleonyx brevis* as a species distinct from *C. variegatus* (fide Kluge, 1962); *Cyrtodactylus* and *Gymnodactylus* as distinct genera (fide Underwood, 1954); *Diplodactylus* and *Lucasium* (*Lucasius*) as congeneric (fide Kluge, MS); *Gehyra punctata* as a species distinct from *G. variegata* (Glen M. Storr, personal communication); *Gymnodactylus milii* and *G. sphyrrurus* (= *Phyllurus milii* and *P. sphyrrurus*; fide Kluge, MS); *Hemidactylus albofasciatus* (= *Teratolepis albofasciata*; Jerry A. Anderson, personal communication); *Phyllodactylus guentheri* as a species distinct from *P. marmoratus* (James R. Dixon, personal communication); *Ptenopus garrulus maculatus* = *P. garrulus*; fide Brain, 1962a). Justification for the many new combinations in *Diplodactylus* can be found in Kluge (MS).

Scleral ossicle counts always indicate the number of elements encircling a single eyeball unless otherwise stated. In the data section on the number of scleral ossicles (pp. 20-31) the average deviations of the mean ossicle counts of the genera were calculated from the following formula:

$$\frac{\bar{x}_1 - \bar{x}_2}{n}$$

in which \bar{x}_1 is the mean of the species in the subfamily, \bar{x}_2 is the mean of the species in the genus, and n is the number of genera in the subfamily.

THE FAMILY GEKKONIDAE

THE GEKKONIDAE AND THE limbless, snake-like lizards of the family Pygopodidae (and, tentatively, the Dibamidae and the Anelytropsidae) have been grouped together in the infraorder Gekkota by Underwood (1957). Underwood has discussed in detail more than 40 morphological similarities between the gekkonids and the relatively more highly specialized pygopodids. The numerous similarities strongly suggest a close relationship between the two groups and support their placement together in the Gekkota. Despite the obvious affinity between the two families, Camp (1923) and Underwood have pointed out that the absence of the *M. rectus superficialis* in gekkos and its presence in pygopods precludes the possibility that the latter group of lizards were derived directly from a gekko stock. The importance of this muscle in the determination of saurian relationships may be somewhat lessened if not totally discounted, however, when its developmental plasticity is considered (Maurer, 1896, 1898; Camp, 1923). Also, it is possible that, if the genotype for the *M. rectus superficialis* was present in a heterozygous (polyallelic) form in most (maybe all) of the main lines of squamate evolution, segregation within the descendent gene pools could account for the peculiar distribution of the muscle among modern groups (e.g., in the Ascalabota it is present in the Pygopodidae, Dibamidae, Xantusiidae, and some Agamidae—*Uromastix*, *Physignathus*, and *Liolepis*; Camp, 1923; Underwood, 1957, p. 240). This reasoning follows that given by Throckmorton (1965)

for certain characters in *Drosophila*, and, as he stated (p. 225), "In the genetic sense, the genotypes responsible for the character states will be *completely homologous*, if not virtually identical; but the character will *appear* many times independently, which is to say that it can occur independently in species derived from species that *did not* show the characteristic, even though the genotype for the character was potential within their gene pools."

The absence of a supratemporal arch readily distinguishes the Gekkonidae from all other lizards of the suborder Ascalabota, which includes the Ardeosauridae, Xantusiidae, Iguanidae, Agamidae, and Chamaeleonidae. The living Gekkota have retained some primitive morphological features (Camp, 1923) and, with the infraorder Iguania (which includes the Iguanidae and Agamidae), are considered by most students of reptilian evolution to be the oldest surviving lizards. The gekkonid stock appears to have differentiated very early in saurian evolution; it has retained only a relatively few generalized features and in the main is very specialized (Romer, 1956).

It is necessary to describe the family Gekkonidae in detail in this section, so that its relationships to the other members of the Gekkota can be more accurately interpreted in future studies. This characterization represents a summary of the information presented by Underwood (1954, 1957) and Romer (1956) and additional data accumulated by me.

FAMILY GEKKONIDAE

CHARACTERIZATION: Skull generally depressed and broad, dermal bones usually very thin, rarely sculptured; osteoderms occasionally present; postorbital and supratemporal arches absent; premaxilla developing from one or two centers of ossification, paired condition persisting in some adults; nasals generally paired; frontal rarely paired in adults; descending processes of frontal (which meet and fuse ventrally and are underlain by

a low, very thin, interorbital septum) surrounding olfactory lobes; supraorbital rarely present; postfrontal present; postorbital absent (possibly fused to postfrontal); parietal foramen absent; parietals greatly expanded, generally paired; supratemporal rarely present; squamosal occasionally absent; quadrate relatively large, complex, generally articulating with opisthotic, rarely with prootic; lacrimal absent (?); jugal almost invariably

present, reduced, in many cases rudimentary; vomers broad, platelike, generally convex below, fused or paired, set at higher level than posterior palatal elements and only barely touching border of palatines; paleochoanate palate-vomer and maxilla not touching or overlapping; pterygoid touching maxilla or nearly so; interpterygoid vacuity broad, extending forward to vomers; large bony shelf extending between basitrabecular process and prootic; pterygoid flange well developed; ectopterygoid small, rodlike, projecting dorso-posteriad; parasphenoid rostrum very small or absent; anterolateral wall of cranial vault formed by prootic; prootic not bordering parietal or does so but slightly; paroccipital process of opisthotic almost invariably present. Stapes generally perforate; internal process of extracolumella present or absent. Scleral ossicles 12 to 40. Angular generally absent; surangular almost invariably fused with articular and prearticular; splenial rarely lost, when present confined to inner middle section of jaw; Meckelian canal completely surrounded by dentary. Teeth pleurodont, homodont, typically small, numerous, cylindrical, and pointed; teeth confined to marginal series on dentary, premaxilla, and maxilla, absent from palatine and pterygoid; two egg teeth present in oviparous species. Second visceral arch discontinuous, except in *Coleonyx*; second ceratobranchial completely absent or moderately long; second epibranchial almost invariably in contact with skull; hyoid arch generally continuous; hyoid cornu rarely absent; inner proximal ceratohyal projection present or absent. Clavicles generally expanded, perforate; interclavicle extremely variable in shape; two well-developed scapulo-coracoid fenestrae, rarely emarginate; sternal fontanel present in some cases; one to three sternal ribs. Vertebrae short, ventrally nearly square in outline, centrum cylindrical, slightly constricted in middle; procoelous or amphicoelous, some intermediate; procoelous condyle narrower than body of centrum; generally 25 to 28 presacral vertebrae; two sacral vertebrae generally present, rarely three or four; trunk vertebrae with continuous notochord in adults and small, free intercentra; paired subcentral foramina present; neural arches of atlas paired or fused; tail rarely

prehensile; caudal vertebrae extremely variable in number; generally four to six non-autotomic postsacral vertebrae immediately posterior to sacrum; septa, except in *Nephrurus asper*, present in caudal centra, septa concentrated regionally or found throughout; postparapophyseal mode of autotomy; chevrons free, intercentral. Limbs well developed; generally five digits; fifth metatarsal short and broad, receiving spinous projection of metatarsal IV; intermedium absent; paraphalangeal elements present in many species with dilated digits; claws rarely absent. Cloacal bones rarely absent, when present, one or two pairs.

Body almost invariably flattened; skin usually soft, rarely adherent to skull; head scalation asymmetrical. Choanae without separate opening for well-developed vomeronasal organ, lacrimal duct opening into canal of vomeronasal organ, and choanal folds leading to same canal. Tongue fleshy, only slightly extensible, covered with small imbricate protuberances distally and large villose papillae proximally, tip uncleft or slightly cleft. Eyes usually extremely large; spectacle (brille) generally present, movable (true) eyelids almost invariably absent; mobile vertical iris generally present; visual cells without oil droplets; single visual cells (type A) and standard saurian double cells (type B) alternating in horizontal rows; peculiar double elements (type C) also present; fovea present or absent. Tectorial membrane originating on large marginal lip of cochlea. Scales of lips bearing scale (lenticular) organs. Endolymphatic sac usually protruding from cranial vault between parietal and opisthotic elements, or through vagus foramen; sac greatly enlarged and calcified in neck region between skin and superficial musculature. Proximal belly of *M. biceps brachii* simple. Preanal pores generally present in males, rarely in females. Hemipenis forked, cuplike. Postcloacal sacs generally present. Digits frequently undilated—either straight or angulate; if dilated, lateral fleshy expansion extending throughout length of digit; in some cases only middle or distal, or both, parts of digits dilated; pilose friction pads commonly present on digits; terminal subcaudal pilose pads rarely present; if present, invari-

ably associated with arboreal activity. Nearly all oviparous, laying one or two hard-shelled eggs. *Heteropholis*, *Hoplodactylus*, and *Naultinus* bearing living young. Generally nocturnal; if diurnal, species having either cranial or peritoneal pigmentation or both. Ability to vocalize generally present.

RANGE: Circumglobal between latitude 50° S. and latitude 40° N. in the New World and latitude 50° S. and latitude 50° N. in the Old World (map 1). Within this band gekkos are found on all major land masses and on a majority of oceanic islands.

FOSSIL HISTORY: It is now clear from the recent works of Hoffstetter (1962; 1964) that the lacertilian fauna of the Upper Jurassic was greatly varied (more than 15 genera and 21 species have been recognized) and that the major evolutionary lines within the Sauria were established by Middle Mesozoic. Hoffstetter's most recent paper (1964) has a direct bearing on the interpretation of the evolution of the Gekkonidae; for this reason his work is briefly reviewed here.

Hoffstetter recognized the three Jurassic genera (*Ardeosaurus* H. von Meyer and *Eichstaettisaurus* Kuhn from Bavaria, and *Yabeinosaurus* Endo and Shikama from Manchuria) as closely related to one another and representatives of the Gekkota, within which he included them in the superfamily Gekkonoidea. Further, he placed the three genera in the family Ardeosauridae (natural assemblage according to Hoffstetter) and defined it on the basis of the following characters: (a) premaxillaries paired; (b) complete supratemporal arch, consisting of two ossified supratemporal elements; (c) supratemporal fenestra open; (d) jugal greatly extended dorsoposteriorly (in this manner the orbit is encircled by a complete bony ring, or with a slight opening posteriorly, as in *Yabeinosaurus*); (e) parietals fused or partially so; (f) pineal foramen present and occupying a central position in the body of the parietal; (g) vertebrae procoelous (not verified for *Eichstaettisaurus*); and (h) completely developed limbs, fifth metatarsal bent, and a phalangeal formula of 2-3-4-5-3 (hand) and 2-3-4-5-4 (foot). Hoffstetter also suggested that the Bavarian genera *Bavarisaurus* Hoffstetter and *Palaeolacerta* Cocude-Michel may be gekkonoids and related to the Ardeo-

sauridae on the basis of their possession of characters a-e and h listed above for that family. For the genera *Bavarisaurus* and *Paleolacerta* he proposed the subfamily Bavarisaurinae which differs from the Ardeosaurinae only in the type of vertebrae (amphicoelous in the former subfamily and procoelous in the latter).

Hoffstetter considered the Ardeosaurinae to be "ancestral gekkonoids," but he did not visualize the subfamily as directly ancestral to the Gekkonidae because of the single or only partially paired parietal and the presence of procoelous vertebrae (he considered both characters advanced). The Eublepharinae, clearly the most primitive living gekkonid subfamily (see later discussion), also exhibit these characteristics, and it seems likely that they are best treated as primitive features of the Gekkonoidea. Hoffstetter also stated that the condition of paired premaxillaries in the Ardeosauridae differs from that of all modern Gekkota. However, as is shown below in this study, it is also characteristic of the primitive eublepharine and diplodactyline gekkos. The discontinuous postorbital arch of *Yabeinosaurus* may indicate the forerunner of that condition found in all Gekkonidae. The absence of a pineal foramen from the bavarisaurine genera (present in the Ardeosaurinae) also overcomes a major obstacle in relating the Ardeosauridae to the Gekkonidae, since this foramen is also absent from the latter family. The large perforation at the frontal-parietal suture in *Paleolacerta* may represent a juvenile developmental stage of the parietal and not the position of the iguanine pineal foramen.

Young (1959) tentatively placed the fragmentary Upper Jurassic *Changisaurus microrhinus* from South Chekiang, China, in the family Gekkonidae. From our present knowledge of the osteology of the Gekkonidae (Romer, 1956) it appears that *Changisaurus* cannot be referred to this family. Baird (1964) has shown that it is not a gekko and suggested that it is a juvenile specimen of the extinct pleurosternoid turtle family Thalassemydidae.

Hoffstetter (1946) described three genera of gekkos from the Tertiary of France: *Rhodanogekko vireti* from the Eocene, *Caudurogekko piveteaui* from the Eocene-Oligocene,

and *Gerandogekko arambourgi* and *G. gailardi* from the Miocene. The lack of important diagnostic features on the available material makes it very difficult to place these three genera in any one of the four subfamilies recognized in the present study. The presence of sculpturing (or osteoderms?) on the frontal of Hoffstetter's *Rhodanogekko* is similar to the condition found in a few gekkonine genera, such as *Geckonia* and some adults of *Pachydactylus*. The splenial impression on the inner surface of the dentaries of *Caudurogekko* and *Gerandogekko* indicates that these genera are not related to the Sphaerodactylinae, because the splenial is consistently absent from this subfamily. The extreme width of the frontal, between the orbits, of *Gerandogekko* is similar to the condition found in many of the Gekkoninae and some of the Diplodactylinae, but unknown in the Eublepharinae and Sphaerodactylinae. The presence of amphicoelous vertebrae in *Gerandogekko* definitely excludes it from any relationship with the completely procoelous Eublepharinae and probably the Sphaerodactylinae which are almost completely procoelous. These data taken together, although admittedly scanty, suggest that the three genera are probably more closely related to the Gekkoninae than to the other subfamilies.

A single incomplete maxilla of a gekko is known from the Miocene of Florida (Estes, 1963). I have examined this material and can refer it to the family Gekkonidae, but not to a particular subfamily, because of the lack of diagnostic features on the maxilla. In addition, the remains of two unidentified small gekkonids have been found in the Miocene deposits of Beni Mellal, Morocco (Hoffstetter, 1961).

The known Tertiary genera of gekkos exhibit very few differences from modern forms (Hoffstetter, 1946, 1961; Estes, 1963), which suggests that the major changes associated with the evolution of the Gekkonidae occurred at a much earlier time. This evidence, coupled with the suspected relationships between the gekkos and the Jurassic Ardeosauridae, adds further support to the antiquity ascribed to the family Gekkonidae.

Hoffstetter (1946) described the genus *Macrophelsuma* from subfossil material of the following modern species from the Mascarene Islands: *M. newtoni*, Rodriguez Island; and *M. cf. guentheri*, Mauritius Island (today known only from Round Island, about 25 kilometers northeast of Mauritius). Hoffstetter's key diagnostic feature of *Macrophelsuma*, that of fused parietals, cannot be used to separate it consistently from *Phelsuma*. Parietal fusion appears to be a function of age in these two groups of species, and therefore I consider *Macrophelsuma* to be congeneric with *Phelsuma*. In the same Mascarene Island collection Hoffstetter recorded the presence of modern *Phelsuma cepediana* and *Hemidactylus cf. frenatus*.

Hecht (1951) described the extinct species *Aristelliger titan* from the Pleistocene or sub-Recent of Jamaica; however, Etheridge (1965a) has suggested that it is conspecific with the modern *Aristelliger lar*. Hecht (1951) and Etheridge (1964, 1965a) have found *A. lar* in sub-Recent and Pleistocene cave deposits in Haiti and the Dominican Republic and the modern *Thecadactylus rapicauda* in Pleistocene deposits of Barbuda, the West Indies. Hecht (1951) also reported on the presence of modern *Aristelliger praesignis* from Pleistocene or sub-Recent cave deposits in Jamaica. On the basis of a single dentary, Koopman and Ruibal (1955) noted the presence of *Tarentola americana* in a cave deposit of possible pre-Columbian age from Cuba. More recently, Etheridge (1965b) has recorded *T. americana* in a Late Pleistocene fauna from New Providence Island, Bahamas.

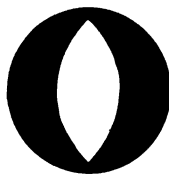
At least three gekkonid lizards have been found preserved in resin: *Platydictylus* (?) *minutus* Giebel (1862), *Hemidactylus viscatus* Vaillant (1873), and *Hemidactylus* (*Lygodactylus*) *capensis* (Peters, 1865, 1866; Cope, 1868). The first two species are considered extinct, whereas the last form is believed to be conspecific with a modern species. Unfortunately, the age of the resin and the locality at which it was collected are obscure, with the exception of Peters' material that came from Zanzibar.

THE SUBFAMILIAL CLASSIFICATION

FEW ATTEMPTS HAVE BEEN MADE to organize into natural groups the many genera of gekkonid lizards. The most recent and by far the most comprehensive study is that of Underwood (1954). He amassed a large amount of information and for the first time brought together evidence in support of intergeneric relationships and evolutionary trends. He also proposed some zoogeographical hypotheses. One of Underwood's major points was the delineation of presumed natural assemblages of genera. He recognized three families: the Eublepharidae, the Sphaerodactylidae, and the Gekkonidae. The last family, which contained more than 85 per cent of the genera, was subdivided into two subfamilies, the Gekkoninae and the Diplodactylinae, based on differences in the form of the pupil. His information on the shape of the pupil was obtained almost exclusively from preserved museum specimens. Underwood defined the Gekkoninae as having an emarginate vertical pupil and the Diplodactylinae, a non-emarginate pupil (text fig. 1; pls. 1-5).



GEKKONINAE



DIPODACTYLINAE

FIG. 1. The major types of shape of the pupil characteristic of the Gekkoninae and Diplodactylinae as proposed by Underwood (1954).

SHAPE OF THE PUPIL AS A SYSTEMATIC CHARACTER

As I have discussed in an earlier paper (Kluge, 1964) and elaborate below, the shape of the pupil must be rejected as a diagnostic character differentiating the Gekkoninae from the Diplodactylinae. Because Underwood's evolutionary and zoogeographical hypotheses were in a large part dependent on the constancy of this single character, they too must be reconsidered.

During a 15-month study in Australia, I examined both living and preserved material of almost all the genera and species of gekkos

known to occur there (see Appendix 1). These genera represent Underwood's proposed gekkonine and diplodactyline subfamilial groups. The pupil was studied (1) in living specimens under different light intensities, subdued, moderate, and intense, (2) in freshly killed specimens after either narcotizing with nembutal or freezing, heating, or drowning had been employed, and (3) after different types of preservatives had been used, such as formalin or alcohol or combinations of both. Walls noted as early as 1932 (p. 69) that the shape of the pupil in living animals rarely corresponds to that in the preserved state. In the material studied by me (see Appendix 1) the shape of the pupil varied greatly and did not appear to be correlated with Underwood's definition of the two subfamilies. The variability in certain species (e.g., *Crenadactylus ocellatus*) included both emarginate and non-emarginate types of pupils. It was relatively common to find the two types of pupils in different species in the same genus (e.g., *Diplodactylus*; see pls. 2 and 3). My observations on non-Australian gekkos indicates the presence of pupil shapes that are intermediate between the gekkonine and the diplodactyline types (pl. 4). Some variation in pupil shape in other gekkos has been indicated earlier by Mann (1931), McCann (1955), and Cogger (1964); also see Denton (1956) and Werner (1965). From my observations it appears that the two major subfamilies of gekkos, Gekkoninae and Diplodactylinae, cannot be distinguished from each other on the basis of pupil shape because of variability. In an attempt to delimit phyletic assemblages of genera in the Gekkonidae, I have studied other characters, particularly osteological ones, as discussed below.

ANALYSIS OF CHARACTERS

It is generally agreed, where divergent evolution has occurred, that similarity between organisms indicates a close relationship. In related taxa, the character-states that are homologous are those that were present in their common ancestor. When the character-states are dissimilar, at least one has diverged.

This section of the paper is devoted to the determination and distribution of the character-states of 18 characters within the Gekkonidae. Also, the relative primitiveness of the character-states is suggested. The evolutionary trends, from primitive to advanced, are inferred from the following postulates which are listed in order of significance:

1. Character-states similar to those occurring in fossil forms, presumed to be related to the ancestors of the modern groups, are considered primitive.

2. Character-states that are universal or frequent in related modern groups (other families and subfamilies) are considered to be primitive. The more widely the character-state occurs among related taxa, the less likely is it due to multiple parallel evolution (Rule of Parsimony).

3. Character-states that are universal or frequent within the taxonomic unit being studied are considered to be primitive (Rule of Parsimony).

4. Character-states confined to the group of taxa under study and occurring in those having the largest number of primitive features as determined by postulates (1), (2), and/or (3) are also considered primitive. Sporne (1954) has shown that the probability that the character-state is primitive increases very rapidly with the increase in the number of primitive characters with which it is correlated.

a-A. TRUE EYELIDS OR SPECTACLE

Bellairs (1948) demonstrated that the presence of true upper and lower eyelids and absence of a spectacle (brille) in the eublepharine genus *Coleonyx* are similar to the typical saurian condition. It appears that the spectacle of all non-eublepharine gekkos, as in some scincid and teiid lizards, and snakes, evolved from the more primitive upper and lower eyelids through fusion and that extra-brillar fringes are secondary developments. Both the upper and lower extra-brillar fringes may be greatly developed and give the appearance of true eyelids but may be partly or wholly analogous depending on the extent of their development. The presence of true eye-

lids and the lack of a spectacle are considered the primitive condition.

The functional significance of the modification of the upper and lower eyelids into a spectacle in gekkonid lizards has been considered by M. A. Smith (1939) and Walls (1942). It is generally agreed by most herpetologists that the spectacle acts as an outer protective covering for the cornea. The semi-fossorial South African genus *Ptenopus* exhibits a high degree of corneal protection. Not only have the true eyelids fused to form a spectacle, but the upper and lower extra-brillar fringes have become extensively developed and movable and are analogous to true eyelids. *Ptenopus* typifies the degree of corneal protection found in many fossorial-terrestrial desert species of gekkos. Fossorial activity and the wind-blown sand of arid and semiarid regions appear to be particularly injurious to the eyes of terrestrial forms, and it is possible that the spectacle evolved under such a selective pressure. There appears to be little advantage for an arboreal form to have a spectacle. True eyelids are present in (spectacle absent from) all eublepharine genera. True eyelids appear to be absent from (spectacle present in) all of the Diplodactylinae, Gekkoninae, and Sphaerodactylinae. It seems likely that the brille-spectacle condition of these three subfamilies has been derived from the primitive condition exemplified by the Eublepharinae.

b-B. PREMAXILLARY BONE

The premaxilla is the most anterior median dermal element of the skull. In adult Squamata this bone is invariably single, except in the Scincidae, in which it is generally paired, and the Gekkonidae, in some forms of which it is paired. The primitive gekkonid premaxilla appears to have been paired, as inferred from the paired condition found in the ancestral Ardeosauridae (see pp. 12, 13).

There are two types of premaxillary development in gekkonid lizards. The first type, apparently restricted to the Eublepharinae and Diplodactylinae, is shown in figure 2A. The premaxilla is paired at the prehatchling egg-tooth stage in these two subfamilies and doubtless forms from two separate centers of ossification. Figure 2B shows the same paired condition in the viviparous genera of the

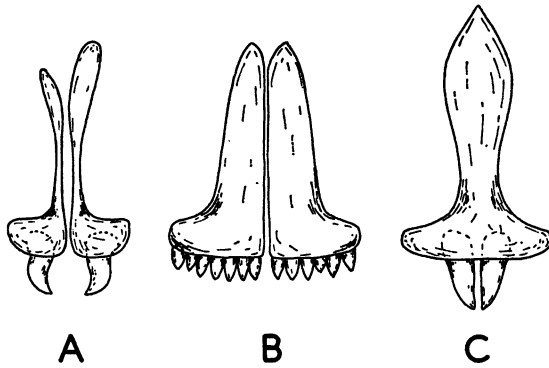


FIG. 2. Anterior view of the premaxilla in pre-hatchling specimens of approximately the same age, showing the paired and single centers of ossification. A. *Coleonyx v. variegatus*, oviparous, with paired egg teeth. B. *Hoplodactylus granulatus*, live-bearer, without specialized egg teeth. C. *Lepidodactylus lugubris*, oviparous, with paired egg teeth.

Diplodactylinae at a stage equivalent to that of the pre-hatchling egg tooth.

The second type of premaxillary development appears to be restricted to the Gekkoninae and Sphaerodactylinae. As shown in figure 2C, at the pre-hatchling egg-tooth stage, the premaxilla is a single element which appears to form from a single center of ossification. I have not been able to find paired centers of ossification at the inception of premaxilla formation by staining with Alizarin red-S.

In adult Eublepharinae and Diplodactylinae either the paired embryonic condition of the premaxilla is retained, or the suture is reduced to a notch or split in the dorsal margin of the nasal process, or lost. In both of the above subfamilies the paired premaxilla and split or notched nasal process was found in 81 per cent of the total number of specimens examined (see Appendix 1). Almost all of the remaining 19 per cent, which showed no indication of the paired embryonic state, were adults of maximum size; apparently bony material had filled in the fissure in the course of aging. Only in a diplodactyline species *Rhynchoedura ornata* was the paired condition evident in juveniles but not in subadults or adults. The absence of any indication of the paired preadult state from *Rhynchoedura* is probably correlated with the extreme nar-

rowness of the nasal process and the formation of the unique birdlike beak.

A split was present in the dorsal margin of the nasal process of the premaxilla in two adult specimens of the gekkonine genus *Rhoptropella* and in one of *Tropicolotes tripolitanus*. Other specimens of different age groups of both of these species show no indication of a split or two embryonic centers of ossification. The few exceptional specimens probably exhibit bone fracturing, a moderately common populational variation without apparent genetic foundation.

It appears that the primitive gekkonoid condition of the premaxilla has been retained in the Eublepharinae, Diplodactylinae, and Ardeosauridae. The single premaxilla found in the Gekkoninae and Sphaerodactylinae seems to have been derived from the paired condition by the loss of the two centers of ossification during a very early stage of embryogenesis.

C-C. ENDOLYMPHATIC APPARATUS

The endolymphatic apparatus of vertebrate animals consists of a narrow canal, the endolymphatic duct, and its terminal enlargement, the endolymphatic sac, which is variable in size and shape. In general, the duct arises from the sacculus of the membranous labyrinth of the inner ear, passes through the endolymphatic foramen into the cranial vault, and expands into the endolymphatic sac. The sac lies in the interdural space in the cranial vault of lower vertebrates (Whiteside, 1922). This space lies between the two layers of the dura mater and is sometimes referred to as the lymphatic space. The endolymphatic sac is a large, thin-walled vesicle surrounded by a connective tissue sheath and appears to develop at a somewhat slower rate than the associated duct. The sac subdivides into numerous small compartments (tubuli) during the course of development and gradually becomes surrounded by a dense vascular network. The tubuli repeatedly divide to give the sac the appearance of a tubular ductless gland. The walls of the sac are glandular and are derived from the labyrinth of the inner ear, the epithelium of which can produce calcareous substances. The production of calcareous materials is

found in the endolymphatic apparatus of all vertebrate classes (Whiteside, 1922).

The endolymphatic sac is filled with an amorphous milky fluid (presumed to be largely calcium carbonate—calcite and aragonite are the more common forms) which hardens upon exposure to air and certain preservatives. Little is known about the properties of the secretion. Sterzi (1899) stated that light was refracted in the fluid form and that the secretion exhibited Brownian movement, but even these initial observations have not been reinvestigated.

The endolymphatic apparatus is basically similar in all vertebrates with the exception of certain ascalabotan lizards. In general, the sac is small and restricted to the cranial vault and to the more proximal part of the vertebral canal; it is almost invariably filled with some calcium carbonate during embryogenesis, and apparently to a greater degree during adult life. In some Ascalabota, Iguanidae (*Aptycholaemus*, *Polychrus* and the anoles, *Anolis*, *Chamaeleolis*, *Chamaelinorops*, *Phenacosaurus*, and *Tropidodactylus*; see Etheridge, MS), and Gekkonidae, the sac becomes greatly enlarged and protrudes from the cranial vault between the parietal and supraoccipital elements (e.g., *Tarentola m. mauritanica*) or through the vagus foramen (e.g., *Gekko g. gekko*) and lies along the surface of the peripheral lateral neck musculature (pl. 5, figs. 2, 3). Camp (1923) reported the presence of calcified sacs in the Xantusiidae (a group of lizards referred to the Ascalabota by some systematists), but I have not been able to verify their presence in any member of that family. The posterior extension of the endolymphatic apparatus from the cranial vault and the presence of calcium carbonate appear to be specializations that have evolved in parallel in the Iguanidae and the Gekkonidae.

The function of the endolymphatic system and its secretion is poorly understood. Early workers (see Whiteside, 1922, for summary) hypothesized that the apparatus regulates pressure in the labyrinth by removing the endolymph from the sacculus, acts as an aid in the transmission of sound waves from the skull into the ear, is analogous to cranial meninges in protecting the central nervous system, and is a source of calcareous material

for bone growth. The question of function is still open for study. For example, Ruth (1918) found some evidence in gekkos to suggest that the sporadic occurrence of the calcareous material in the gland is correlated with the time of eggshell formation, and Kästle (1962), who studied *Lygodactylus picturatus* and *Phelsuma d. dubia*, described the neck swellings as "seasonal" in females. In a presumably analogous situation, however, Etheridge (MS) found no relationship between sex or size and the amount of calcification in two species of the iguanid genus *Anolis*.

Calcified endolymphatic sacs in the postcranial region appear to be absent from all Eublepharinae and Diplodactylinae. The complete absence of the sac in the neck region (i.e., in an uncalcified state), however, must be further investigated histologically in these subfamilies. It appears that in the Gekkoninae and all Sphaerodactylinae postcranial calcified sacs are present (the calcified condition has not been confirmed for the following gekkonine genera: *Agamura*, *Blaesodactylus*, *Saurodactylus*, *Teratoscincus*, and *Thecadactylus*).

Apparently the greatly enlarged postcranial extension of the endolymphatic sac, as found in the Gekkoninae and Sphaerodactylinae, is a specialized condition derived from an intracranial vault form. The different points of exit from the cranial vault, as noted above, suggest the possibility of parallel evolution within the Gekkoninae.

d-D. PREANAL ORGANS AND ESCUTCHEON SCALES

The glandlike preanal organs of lizards have been discussed in some detail by Camp (1923) and M. A. Smith (1935). These organs appear to be simple tubular invaginations of the epidermis, and the secretion is apparently odorless and is believed to be composed chiefly of epidermal scales. It seems that the various nominal groupings of these organs, such as femoral, inguinal, and anal, simply refer to regional concentrations of the same structures; therefore they are all treated here as preanal organs. The homology of the postanal organs in some scincid lizards (e.g., *Tropidophorus*) is questionable. In general, preanal organs appear to be similar to mam-

malian sebaceous glands (Félizet, 1911), although both M. A. Smith (1935) and H. Smith (1960) stated that the structures are not glands, without elaborating on the point. Cole (1966) recently studied histological preparations of these structures from the iguanid *Crotaphytus collaris* and has demonstrated that glandular activity does occur (also suggested by Greenberg, 1943, for *Coleonyx*). It has been recognized for some time that the external orifice (preanal pore) of a single organ is more actively engorged with the waxy cellular debris during certain seasons. The activity seems to be correlated with the sex cycle. Additional evidence supporting such a correlation comes from the fact that the pores are almost exclusively restricted to males and that when present in females they are much smaller and in most cases underdeveloped. The external aperture of the organ occurs either in the center of the scale or at its posterior margin. Homologous scales in females are occasionally indented and suggest the male pore arrangement; however, the epidermal layer is almost invariably imperforate.

Although preanal pores are conspicuous saurian features, the exact function of the organs is poorly understood. Greenberg (1943) has provided the best evidence for their function in gekkonid lizards. He stated that, during courtship in *Coleonyx*, the male rubs the wax cones protruding from the pores transversely across the tail of the female. She responds to the rubbing by elevating her tail, a necessary preliminary to the actual act of copulation. The pores are present in most lizard groups, and presumably they were present in ancestral lizards.

Escutcheon scales (apparently analogous to the callose scales of agamid lizards; M. A. Smith, 1935, pp. 132, 211, fig. 56) are specialized glandular scales lacking pigment on the ventral aspect of the abdominal, femoral, and postcloacal regions (Taylor and Leonard, 1956). These scales are more distinctly modified in males than in females and appear to increase in number with age. It has been suggested by Noble and Bradley (1933) and by Taylor and Leonard (1956) that these scales are structures from which preanal organs in other groups were derived, but there is no clear evidence for this suggestion and it ap-

pears more likely that escutcheon scales evolved from femoral organs (postulate 4; see character-groups, table 2). There is some similarity (almost certainly coincidental) between the general shape of the area covered by escutcheon scales in sphaerodactyline gekkos and the patch of femoral pores found in the diplodactyline genera *Naultinus*, *Heteropholis*, *Hoplodactylus*, *Carphodactylus*, and *Bavayia*. There is no evidence that suggests that the Sphaerodactylinae were derived from the Diplodactylinae, or vice versa. Pasteur (1964) briefly noted that an escutcheon analogue may occur in the gekkonine *Lygodactylus* and related groups, but such has not been verified by further study (Paul Maderson, personal communication). Taylor and Leonard stated that escutcheon scales may serve the same general function as femoral organs.

Preanal pores are present in all eublepharine genera except *Holodactylus*. In the Diplodactylinae, they have been found in 11 out of 23 species of *Diplodactylus* and in all other genera except *Nephrurus* and *Phyllurus* (Kluge, MS). They are absent from the Sphaerodactylinae and approximately one-half of the gekkonine genera. Escutcheon scales appear to be restricted to the Sphaerodactylinae.

It appears that preanal organs have been lost independently in all major gekkonid groups with the possible exception of the Sphaerodactylinae. Furthermore, it seems likely that there has been multiple parallel loss of these organs within the Gekkoninae in view of their absence from so many morphologically different genera. The escutcheon scales of the Sphaerodactylinae are almost certainly modified preanal organs.

e-E. ABILITY TO VOCALIZE

Almost all the characters used in this study are well documented with the exception of the distribution of vocal ability and the number of eggs deposited at a single laying (number of young born in viviparous species, *sensu lato*; see character f-F). These features appear to show considerable promise in the elucidation of the relationships within the family, but, by the very nature of the characters themselves, little information has been accumulated on them. The following discussion

of vocal ability and that on the number of eggs laid are based on cursory observations that I have made during the past six years, both in the field and laboratory, and from a review of the literature. These characters almost certainly will require more detailed future studies.

Among gekkonids, all sphaerodactylines appear to be voiceless, whereas all Eublepharinae and certainly most of the Gekkoninae and Diplodactylinae that have been investigated actively vocalize (Underwood, 1954). It has been suggested by Underwood (1962) that in gekkos there may be a correlation between voicelessness and an environment in which illumination is great enough to permit visual cues, which may explain the condition found in the voiceless, diurnal (shade-inhabiting) Sphaerodactylinae. However, at least some diurnal gekkonines and diplodactylines actively vocalize (e.g., *Naultinus*). The presence of vocal ability probably represents the primitive character-state in gekkonids as inferred from its distribution among the more primitive subfamilies, Eublepharinae, Diplodactylinae, and Gekkoninae (postulate 4). The absence of this character-state from the Sphaerodactylinae and non-gekkonids probably represents a condition arrived at in parallel.

f-F. NUMBER OF EGGS LAID

For introductory remarks on the number of eggs laid, see character e-E (Ability to Vocalize). All the Eublepharinae that I have been able to observe lay two eggs. The Diplodactylinae also lay two eggs with the exception of the three New Zealand genera, *Heteropholis*, *Hoplodactylus*, and *Naultinus*, which bear living young. So far as known, all the Sphaerodactylinae lay one egg, and the Gekkoninae lay two (*Aristelliger* is exceptional in laying only one). The laying of a single egg may be related to small adult size in the Sphaerodactylinae, but the smaller gekkonine genera that I have studied (e.g., *Lygodactylus*) do not follow this hypothesis. In the sphaerodactyline genera *Gonatodes* and *Sphaerodactylus*, both right and left ovaries and oviducts are fully matured and appear to alternate in the production of a single egg. The laying of two eggs is probably the primitive character-state in the Gekkonidae (as inferred from postulate

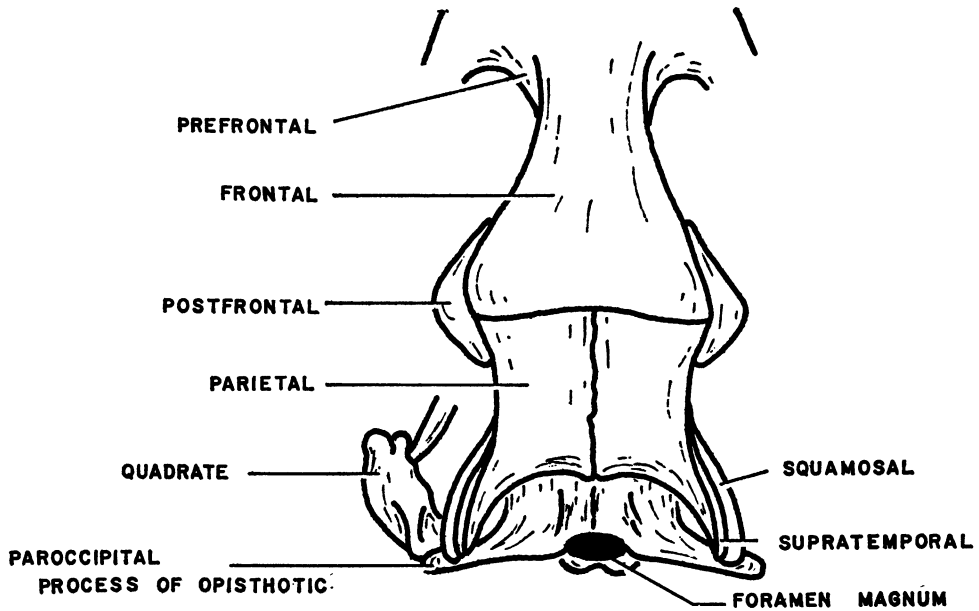
4). The reduction in egg number in the Sphaerodactylinae and the presence of viviparity in the Diplodactylinae are considered advanced character-states.

g-G. SUPRATEMPORAL BONE

The application of the names "supratemporal" (=tabular) and "squamosal" to the two small dermal temporal elements in reptiles was extensively reviewed by Camp (1923). From the observations of Underwood (1957) and Kluge (1962) and additional information presented here, it appears that the squamosal (the lateralmost element) persists and the more medial supratemporal has been lost in most gekkonid lizards. These findings are in contradiction to Camp's supposition that the supratemporal persists and the squamosal is lost. Camp, who lacked the critical material, was unaware of the evolutionary sequence in the Eublepharinae (Kluge, 1962) that conclusively shows the loss of the supratemporal (the inner element) and the persistence of the squamosal (e.g., in *Eublepharis macularius* and *E. kuroirwae orientalis* the squamosal is large and the supratemporal is small, in *E. hardwickii* the squamosal is large but the supratemporal has been finally lost; fig. 3). The presence of the supratemporal is doubtless the primitive character-state in gekkonid lizards (Romer, 1956).

The supratemporal and squamosal strengthen the complex quadrate-opisthotic-parietal articulation. Maximum strength is attained when both the supratemporal and the squamosal are present, the minimum when both elements are absent.

The supratemporal was found in the Eublepharinae in both species of *Aeluroscalabotes*, *Eublepharis macularius* and *E. kuroirwae orientalis*, and in *Holodactylus africanus*. The absence of the supratemporal has been confirmed from the Eublepharinae in *Eublepharis hardwickii*, from both *Hemitheconyx* species (wrongly stated by Underwood, 1957, as being present in *H. caudicinctus*), and from all *Coleonyx*. The supratemporal is absent from all of the Diplodactylinae, Gekkoninae, and Sphaerodactylinae. It seems reasonable to suggest that the supratemporal was lost in the ancestral stock leading to the latter subfamilies, and the loss did not happen inde-



ORDER OF EVOLUTIONARY CHANGE

- | | |
|---------------------------|--|
| 1. SUPRATEMPORAL — | LOST |
| 2. SQUAMOSAL — | LOST |
| 3. PAROCCIPITAL PROCESS — | GREATLY REDUCED, ULTIMATELY
LOST |
| 4. QUADRATE — | MOVES UNDER PARIETAL,
ARTICULATES WITH PROTIC |

FIG. 3. Evolution of the temporal region in the Gekkonidae. Dorsal view of the posterior portion of the cranium of a hypothetical primitive gekko, with the major cranial bones and other points of reference indicated. The order of evolutionary change from primitive to advanced is listed below the drawing.

pendently in the three groups. As inferred from the character groupings, it is possible that this loss occurred within the Eublepharinae.

h-H. NUMBER OF SCLERAL OSSICLES

Scleral ossicles are small, thin, ossified, cartilaginous plates embedded in the scleroid coat of the eyeball (Edinger, 1929). They form an interrupted or continuous ring of one to 40 elements radiating from the edge of the cornea. These plates should not be confused with the cartilaginous orbital cup, which occasionally also ossifies, but lies completely outside the eyeball proper. It is now believed that scleral ossicles are neomorphic elements

that developed directly from the scleroid layer (Romer, 1956) and are not, as once thought, homologous to the circumorbital ring of dermal bones of primitive vertebrates. Fossil evidence suggests that a ring of bony plates was present in primitive vertebrates and has been maintained in all main lines of evolution, although in living forms they are with certainty known only in actinopterygian fishes, birds, and most reptiles (Piveteau, 1955, 1966). Scleral ossicles have not been found in chondrichthyan fishes, modern crocodylians and mammals, or snakes. They are presumed to be absent from modern amphibians, although small, irregularly shaped bony elements have been found in a salaman-

drid salamander (*Cynops pyrrhogaster* subsp.) and a microhylid frog (De Beer, 1937; Walls, 1942), but here the homology is questioned. The apparent parallel loss of these structures in the differently adapted major vertebrate groups is difficult to explain on the basis of a common adaptive shift due to similar forces of natural selection. The function of scleral ossicles is still unsolved. Walls (1942) considered that at least for sauropsidian (reptile and bird) vision they assist in accommodation by maintaining the over-all shape of the eyeball. In some birds they appear to maintain the asymmetry of the eyeball so that binocular vision can be realized (Slonaker, 1918).

Apparently the number of scleral ossicles has never been considered a major diagnostic character in any of the vertebrate classes. It is therefore surprising that in a relatively small group, such as the Gekkonidae, ossicles appear to be a significant indicator of relationships. The extreme numerical differences among the gekkonid subfamilies may provide the necessary material for a better understanding of the function of these elements in all vertebrates.

Gugg's (1939) comprehensive study of modern rhynchocephalian and lepidosaurian ossicles suggests that the primitive number may be about 14. The number of ossicles varies very little in lepidosaurians with the exception of some gekkonids. All the ossicle data on gekkonid lizards compiled in the present study is included in table 1. Additional ossicle counts can be obtained from Underwood's (1954, 1957) general studies on gekkos and pygopodids, and from the works of Stephenson (1960) and Stephenson and Stephenson (1956) on Australian and New Zealand gekkos, respectively. In obtaining the ossicle numbers given in table 1, I counted all the bony plates, including the occasionally much-reduced dorsal and ventral elements. Care was taken, however, not to count the splinter-like fragments produced by extraction of the eyeball from its socket. The greatest degree of accuracy in counting the ossicles is achieved by using preserved specimens, before they have been cleared and stained.

EUBLEPHARINAE: All of the five recognized eublepharine genera (Underwood, 1954) were examined, including 11 species and subspecies

represented by 111 eyeballs. The range of variation is 13 to 25 ossicles, with a mean of 16.7 and 2.7 as the average deviation of the means of the genera (fig. 4). The mean of 16.7 is not truly representative of the subfamily, because *Coleonyx*, the genus with the lowest number of ossicles, is represented by the greatest number of specimens: 96 specimens of *Coleonyx* as compared to seven of *Eublepharis*, the next highest. The mean for *Coleonyx* alone is 16.1. I believe that this is the result of a secondary reduction from a higher, more primitive eublepharine number, possibly represented today by that of *Aeluroscalabotes*. Some support for this thesis is gained from the following points: (1) on the basis of the large number of other characters (see remaining discussions of subfamilial diagnostic characters), *Aeluroscalabotes* is considered to be the most primitive surviving eublepharine genus and very near the ancestral stock of the subfamily, and it therefore seems reasonable to assume that the higher number is part of the primitive genetic background of the group; (2) the nearest relative of *Coleonyx* is clearly the slightly more primitive *Eublepharis* (Kluge, 1962) which exhibits a higher ossicle number, approaching that of *Aeluroscalabotes*; and (3) the Diplodactylinae exhibit extremely high ossicle numbers and are believed to have been derived from a primitive eublepharine, possibly near *Aeluroscalabotes*. It is therefore postulated that the mean ossicle number of 24.0 of *Aeluroscalabotes* is closer to the primitive condition for this subfamily. The remaining four genera appear to show stepwise reductions, culminating in the low number of *Coleonyx*, which only coincidentally approximates the common lacertilian number of 14.

DIPLODACTYLINAE: All the 14 genera that I have referred to the Diplodactylinae have been examined. Of these 14 genera, counts were accumulated on 44 species and subspecies, represented by 260 eyeballs. The range of variation is 21 to 40 ossicles per eyeball, with a mean of 31.9 and 3.8 as the average deviation of the means of the genera (fig. 4).

Stephenson (1960), after studying small numbers of juvenile and adult specimens of *Nephrurus*, suggested that the ossicle number decreased with age. From Stephenson's ac-

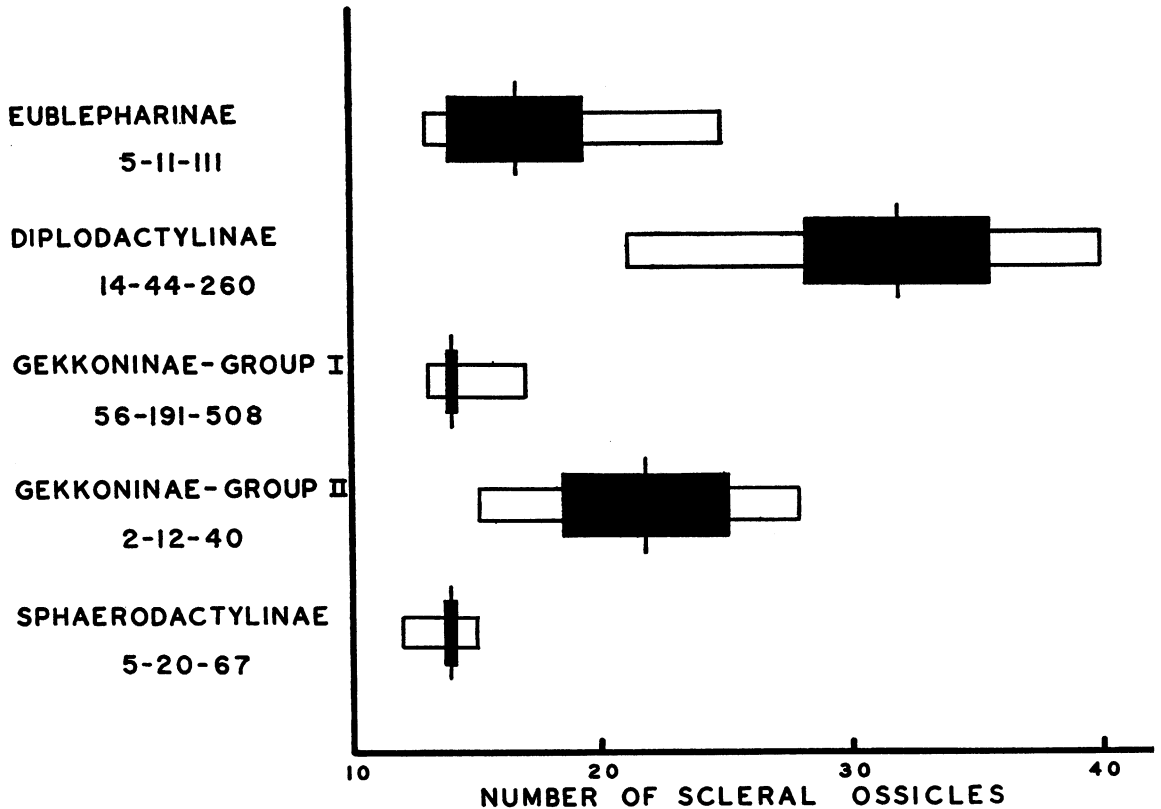


FIG. 4. Range of variation, mean, and average of the deviations of the means of the genera for the Eublepharinae (five genera, 11 species and subspecies, 111 specimens examined), Diplodactylinae (14 genera, 44 species and subspecies, and 260 specimens examined), Gekkoninae Group I (56 genera, 191 species and subspecies, and 508 specimens examined), Gekkoninae Group II (two genera, 12 species and subspecies, and 40 specimens examined), and Sphaerodactylinae (five genera, 20 species and subspecies, and 67 specimens examined).

count it was not clear if the reduction occurred by loss or fusion. My observations, however, do not support the contention that ossicles are lost or fused in ontogeny in any species. Counts on *Phyllurus milii* (fig. 5), a member of the genus most closely related to *Nephrurus* (Kluge, MS), indicate that there is almost as great a degree of variation in a single individual (comparing right and left eyeballs) as there is between juveniles (snout-to-vent length, 38 mm.) and adults (89 mm.). An analysis of variance was applied to the data in figure 5, and it was concluded that the estimated variance between the column means (snout-to-vent lengths for 28, 29, 30, and 31 scleral ossicle counts) is significantly less (at $P=0.001$) than the estimated variance within the columns: $F=2.282$, $n_1=3$,

$n_2=18$. A corner test of association also indicated that the number of ossicles does not decrease with age in *Phyllurus milii*. All the specimens of *P. milii* used in this example are from a single deme at Bakers Hill, Western Australia.

The Diplodactylinae show affinity to the Eublepharinae by reason of their increase in ossicle number; it is proposed that both subfamilies were derived from an ancestral form that possessed an ossicle number higher than 14. The more primitive diplodactyline genera, *Crenadactylus*, *Eurydactylodes*, *Heteropholis*, *Hoplodactylus*, *Naultinus*, and *Phyllurus* (Kluge, MS), exhibit mean scleral ossicle counts in the low- to mid-twenties (range 21 to 29) around that of the most primitive eublepharine genus *Aeluroscalabotes* (23 to

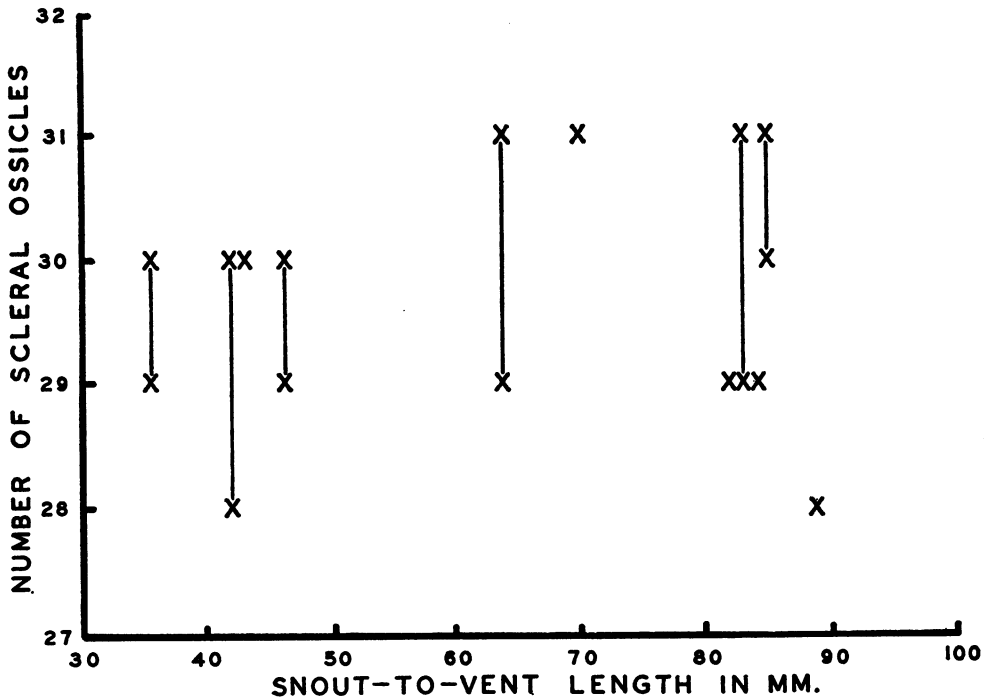


FIG. 5. Number of scleral ossicles (X) graphed against snout-to-vent length in 11 juvenile and adult *Phyllurus miii* from Western Australia. In those cases in which the number of ossicles is different in the two eyeballs from the same individual, they are connected by a vertical line to indicate the range of variation in that individual.

25). This correlation may suggest that the ancestral number of the Diplodactylinae was in the low- to mid-twenties.

GEKKONINAE (GROUP I): Included in this group are 56 genera and 191 species and subspecies, represented by 508 eyeballs. The range of variation is 13 to 17, with a mean of 14.0 and 0.2 average deviation of the means of the genera (fig. 4).

Stenodactylus lumsdenii, *S. orientalis*, and *S. maynardi* belong to Group I and are referred to the genus *Crossobamon*. *Crossobamon*, with these three forms included, has a great deal of external morphological and osteological uniformity, almost certainly indicative of a natural assemblage of species. The genus is characterized by (1) straight, undilated digits, with a lateral fringe or denticulation of pointed scales, subdigital surfaces covered with transverse lamellae; (2) nasal region not noticeably swollen; (3) dorsal body scalation heterogeneous, consisting of granules and scattered, enlarged, keeled tubercles; (4) preanal pores almost invariably present

in males; (5) scleral ossicles 14 or 15; (6) angular absent; and (7) squamosal present. In accord with the morphological uniformity of the species, the geographical range of the genus appears to be continuous through Afghanistan, Iran, West Pakistan, and Turkestan.

GEKKONINAE (GROUP II): Group II consists of two genera, *Stenodactylus* and *Teratoscincus*, of which 12 species and subspecies, represented by 40 eyeballs, have been examined. The range of variation in number of ossicles is 15 to 28, with a mean of 21.7 and 3.4 average deviation of the means of the genera (fig. 4). The ossicle number was not determined for *Stenodactylus arabicus* (= *haasi*), but, on the basis of its external morphological similarity and geographical proximity (Haas, 1957; Anderson, 1896), it also appears to belong to this group.

All the species thus far examined in Group II exhibit some similarity in the shape and scalation of the digits, as well as in an increased ossicle number. These characters

taken together seem to indicate that the species form a natural group. The increased ossicle number found in this assemblage may have arisen directly from that of the Eublepharinae and Diplodactylinae. The presence of the angular in *Teratoscincus* (a primitive gekkonid feature found elsewhere only in the Eublepharinae) strongly supports this contention. If confirmed, the absence of a calcified postcranial extension of the endolymphatic apparatus from *Teratoscincus* (although present in *Stenodactylus*) can also be cited as additional evidence. The correlation between the largest ossicle number of Group II and that of the Eublepharinae and that of the more primitive diplodactyline genera (*Crenodactylus*, *Eurydactylodes*, *Heteropholis*, *Hoplodactylus*, *Nautilinus*, and *Phyllurus*; see table 1) is considered significant.

The two genera that belong to Group II (*Stenodactylus* and *Teratoscincus*) are easily distinguished from each other osteologically. The angular is absent from the former genus and present in the latter, and the squamosal is present in the former genus and absent from the latter (see subfamilial diagnostic character discussions of the angular and squamosal). These osteological differences suggest that the group, if a natural one, has been isolated for a relatively long period of time.

On the basis of their large number of external (meristic and mensural) and internal morphological similarities, I have transferred *Ceramodactylus major*, *Pseudoceramodactylus khobarensis*, and *Trigonodactylus arabicus* to *Stenodactylus* (see table 1). *Stenodactylus arabicus* Haas (1957, p. 56) is preoccupied by *Stenodactylus (Trigonodactylus) arabicus* Haas (1957, p. 51). I here propose the name *haasi*, *nomen novum* for *arabicus* Haas (1957, p. 56). *Stenodactylus* is now defined by the following characters: (1) digits relatively long, straight, variable in width, bordered by lateral fringe of pointed scales, subdigital scales small, carinate or triangular, transverse lamellae absent; (2) nasal region usually markedly swollen; (3) dorsal body scalation homogeneous, consisting of smooth or pointed granules; (4) preanal pores almost invariably absent from males; (5) scleral ossicles 20 or more; (6) angular absent; and (7) squamosal present. Geographically, this expanded genus

now contains a well-circumscribed group of species restricted to the Sahara Desert and eastern coast of Africa, as far south as Kenya, to Arabia, Iraq, Israel, Jordan, Lebanon, and Syria.

SPHAERODACTYLINAE: All the five genera that are referred to this subfamily have been examined. This includes 20 species and subspecies, represented by 67 eyeballs. The range of variation of the number of ossicles is 12 to 15, with a mean of 14.0 and 0.1 as the average deviation of the means of the genera (fig. 4).

In summary, it appears that the primitive scleral ossicle number in gekkonid lizards was in the low- to mid-twenties; this condition has been retained in three distinct evolutionary lines. The more primitive eublepharines, *Aeluroscalabotes* and *Eublepharis*, seem to have retained the primitive number, whereas the other genera in the subfamily (particularly the specialized *Coleonyx*) exhibit stepwise reductions in ossicle numbers. In contrast to this trend in the Eublepharinae, the more specialized genera in the Diplodactylinae (second evolutionary line) show a marked increase in ossicle number which culminates in 40 per eyeball. The gekkonine Group II, which includes only *Stenodactylus* and *Teratoscincus*, represents the third evolutionary line. The significantly lower ossicle numbers found in the Gekkoninae (Group I) and Sphaerodactylinae were probably derived from an ancestral condition in the low- to mid-twenties. The trend in the reduction of the number of ossicles in the Eublepharinae may indicate the steps by which the Gekkoninae (Group I) and Sphaerodactylinae reverted to near the "standard" lacertilian number of 14. The selective pressure that holds the Gekkoninae and Sphaerodactylinae to this lower number may not be so strong as that acting on most other non-gekkonid lizards, as inferred from the degree of ossicle variation found in the two subfamilies.

i-I. CLOACAL SACS AND BONES

Cloacal sacs are moderately large, paired invaginations situated slightly posterior to the vent. The distance between the external orifice of the sac and the vent varies markedly in different species. These pockets are unique to the Gekkota. They are invariably

TABLE 1
 THE NUMBER OF SCLERAL OSSICLES PER EYEBALL IN THE SUBFAMILIES EUBLEPHARINAE,
 DIPLODACTYLINAE, GEKKONINAE, AND SPHAERODACTYLINAE

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
Eublepharinae		
<i>Aeluroscalabotes</i>		
<i>dorsalis dorsalis</i>	4	23-25 (23.8)
<i>felinus</i>	1	25
<i>Coleonyx</i>		
<i>brevis</i>	16	15-18 (16.3)
<i>elegans elegans</i>	2	16
<i>mitratus</i>	2	14-15 (14.5)
<i>variegatus</i> ^a	76	13-19 (16.1)
<i>Eublepharis</i>		
<i>hardwickii</i>	2	17-18 (17.5)
<i>macularius</i>	5	15-19 (17.6)
<i>Hemitheconyx</i>		
<i>caudicinctus</i>	1	18
<i>Holodactylus</i>		
<i>africanus</i>	2	18-22 (20.0)
Diplodactylinae		
<i>Bavayia</i>		
<i>cyclura</i>	3	32-33 (32.7)
<i>sawagii</i>	2	31-34 (32.5)
<i>Carphodactylus</i>		
<i>laevis</i>	4	30-33 (31.8)
<i>Crenadactylus</i>		
<i>ocellatus</i>	16	22-27 (24.3)
<i>Diplodactylus</i>		
<i>alboguttatus</i>	2	33-34 (33.5)
<i>byrnei</i>	2	32
<i>ciliaris ciliaris</i>	5	33-37 (35.0)
<i>ciliaris intermedius</i>	20	30-34 (31.4)
<i>conspicillatus</i>	4	31-34 (32.0)
<i>damaeus</i>	14	37-40 (37.9)
<i>elderi</i>	2	30
<i>maini</i>	4	32-33 (32.8)
<i>pulcher</i>	10	30-38 (34.3)
<i>savagei</i>	2	25-27 (26.0)
<i>spinigerus</i>	9	31-36 (33.3)
<i>steindachneri</i>	2	32
<i>stenodactylus</i>	16	34-39 (36.6)
<i>strophurus</i>	4	31-32 (31.5)
<i>taenicauda</i>	6	30-35 (33.1)
<i>tessellatus</i>	5	34-38 (36.8)
<i>vittatus</i>	24	33-38 (36.3)
<i>williamsi</i>	6	29-35 (32.7)
<i>Eurydactylodes</i>		
<i>vieillardii</i>	1	27
<i>Heteropholis</i>		
<i>tuberculatus</i>	2	21-22 (21.5)
<i>Hoplodactylus</i>		
<i>duvaucelii</i>	6	24-26 (25.0)
<i>granulatus</i>	8	23-27 (25.4)

TABLE 1—(Continued)

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
<i>pacificus</i>	6	26–29 (27.2)
<i>Nautilinus</i>		
<i>elegans</i>	4	22–23 (22.5)
<i>Nephrurus</i>		
<i>asper</i>	4	30–33 (31.5)
<i>laevissimus</i>	2	29–33 (31.0)
<i>levis levis</i>	10	32–36 (34.6)
<i>wheeleri wheeleri</i>	2	32–33 (32.5)
<i>Oedura</i>		
<i>lesueurii lesueurii</i>	4	32–34 (32.5)
<i>marmorata</i>	2	34–35 (34.5)
<i>monilis</i>	2	32–34 (33.0)
<i>robusta</i>	2	31–32 (31.5)
<i>tryoni</i>	2	29–30 (29.5)
<i>Phyllurus</i>		
<i>cornutus</i>	4	25–27 (26.0)
<i>mili</i>	20	28–31 (29.4)
<i>platurus</i>	4	25–28 (26.5)
<i>sphyrurus</i>	2	27–29 (28.0)
<i>Pseudothecadactylus</i>		
<i>australis</i>	2	31–32 (31.5)
<i>Rhacodactylus</i>		
<i>auriculatus</i>	2	29–30 (29.5)
<i>Rhynchoedura</i>		
<i>ornata</i>	8	32–37 (34.6)
Gekkoninae (Group I)		
<i>Afroedura</i>		
<i>pondolia pondolia</i>	2	14
<i>transvaalica platyceps</i>	2	14–15 (14.5)
<i>Agamura</i>		
<i>persica</i>	3	14
<i>Ailuronyx</i>		
<i>seychellensis</i>	2	14
<i>Alsophylax</i>		
<i>pipiens</i>	1	14
<i>Aristelliger</i>		
<i>cochranae barbouri</i>	4	14
<i>praesignis praesignis</i>	6	14
<i>Blaesodactylus</i>		
<i>boivini</i>	2	14
<i>Bogertia</i>		
<i>lutzae</i>	1	14
<i>Briba</i>		
<i>brasiliana</i>	3	14
<i>Bunopus</i>		
<i>tuberculatus</i>	2	14
<i>Calodactylodes</i>		
<i>aureus</i>	2	14
<i>Chondrodactylus</i>		
<i>angulifer</i>	2	15–16 (15.5)
<i>Cnemaspis</i>		
<i>affinis</i>	1	14
<i>africana</i>	1	14

TABLE 1—(Continued)

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
<i>boulengerii</i>	1	14
<i>indica</i>	1	14
<i>kandiana</i>	3	14
<i>kendallii</i>	2	14
<i>nigridius</i>	1	14
<i>ornata</i>	1	14
<i>quattuorseriata quattuorseriata</i>	2	14
<i>siamensis</i>	2	14
<i>wynadensis</i>	2	14
<i>Colopus</i>		
<i>wahlbergii</i>	3	14-15 (14.7)
<i>Cosymbotus</i>		
<i>platyurus</i>	2	14
<i>Crossobamon</i>		
<i>eversmanni</i>	2	14
<i>lumsdenii</i>	1	14
<i>maynardi</i>	3	14-15 (14.3)
<i>orientalis</i>	4	14-15 (14.3)
<i>Cryptodactylus</i>		
<i>agusanensis</i>	1	14
<i>angularis</i>	1	14
<i>annulatus</i>	3	14
<i>baluensis</i>	1	14
<i>brevipalmatus</i>	1	14
<i>caspicus</i>	1	14
<i>cavernicolus</i>	1	14
<i>collegalensis</i>	1	14
<i>condorensis</i>	1	14
<i>consobrinus</i>	1	14
<i>darmandvillei</i>	1	14
<i>feae</i>	1	14
<i>fedtschenkoi</i>	1	14
<i>fraenatus</i>	2	14
<i>fumosus</i> subsp.	1	14
<i>intermedius</i>	1	14
<i>irregularis</i>	1	14
<i>jellesmae</i>	1	14
<i>kachhensis watsoni</i>	2	14-15 (14.5)
<i>khasiensis</i> subsp.	1	14
<i>kirmanensis</i>	1	14
<i>kotschyi</i> subsp.	1	14
<i>kotschyi oertzeni</i>	1	14
<i>lateralis</i>	1	14
<i>lawderanus</i>	1	14
<i>loriae</i>	1	14
<i>louisianensis</i>	2	14
<i>malayanus</i>	1	14
<i>malcolmsmithi</i>	1	14
<i>marmoratus</i>	2	14
<i>mimikanus</i>	1	14
<i>nebulosus</i>	1	14
<i>oldhami</i>	1	14
<i>papuensis</i>	1	14

TABLE 1—(Continued)

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
<i>peguensis</i> subsp.	1	14
<i>pelagicus pelagicus</i>	2	13-14 (13.5)
<i>philippinus</i>	1	14
<i>pubisulcus</i>	1	14
<i>pulchellus</i>	1	14
<i>redimiculus</i>	1	14
<i>rubidus</i>	1	14
<i>russowii</i>	1	14
<i>scaber</i>	2	14
<i>serpensinsula</i>	1	14
<i>stoliczkai</i>	1	14
<i>triedrus</i>	1	14
<i>vankampeni</i>	1	14
<i>wetariensis</i>	1	14
<i>Dravidogecko</i>		
<i>anamallensis</i>	1	14
<i>Ebenavia</i>		
<i>inunguis</i>	2	14
<i>Geckolepis</i>		
<i>maculata</i>	2	14-15 (14.5)
<i>Geckonia</i>		
<i>chazaliae</i>	2	14
<i>Gehyra</i>		
<i>australis</i>	2	14
<i>mutilata</i>	6	14
<i>oceanica</i>	4	14
<i>punctata</i>	20	13-16 (14.2)
<i>variegata</i>	20	14-16 (14.3)
<i>Gekko</i>		
<i>athymus</i>	1	14
<i>chinensis</i>	1	14
<i>gecko gecko</i>	5	14
<i>japonicus</i>	1	14
<i>mindorensis</i>	1	14
<i>monarchus</i>	1	14
<i>palawanensis</i>	1	14
<i>palmatus</i>	1	14
<i>smithii</i>	2	14
<i>subpalmatus</i>	1	14
<i>swinhonis</i>	1	14
<i>vittatus</i>	4	14
<i>Gymnodactylus</i>		
<i>geckoides geckoides</i>	2	14
<i>Hemidactylus</i>		
<i>brookii brookii</i>	4	14
<i>brookii angulatus</i>	2	14
<i>brookii haitianus</i>	10	14-15 (14.3)
<i>flaviviridis</i>	2	14
<i>frenatus</i>	12	14
<i>garnotii</i>	2	14
<i>giganteus</i>	2	14
<i>karenorum</i>	2	14
<i>leschenaultii</i>	2	14-15 (14.5)

TABLE 1—(Continued)

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
<i>persicus</i>	2	14
<i>turcicus turcicus</i>	2	14–15 (14.5)
<i>Hemiphyllodactylus</i>		
<i>typus typus</i>	8	14–16 (14.8)
<i>yunnanensis</i>	5	14
<i>Heteronotia</i>		
<i>binoei</i>	20	14–15 (14.1)
<i>spelea</i>	2	14–15 (14.5)
<i>Homonota</i>		
<i>darwinii</i>	4	13–14 (13.8)
<i>gaudichaudii</i>	4	13–14 (13.5)
<i>horrida</i>	10	14
<i>Homopholis</i>		
<i>fasciata</i> subsp.	2	14
<i>wahlbergii</i>	2	14
<i>Lepidodactylus</i>		
<i>brevipes</i>	2	14
<i>guppyi</i>	3	14–15 (14.3)
<i>listeri</i>	1	14
<i>lugubris</i>	10	14–16 (14.3)
<i>manni</i>	1	14
<i>naujanensis</i>	1	14
<i>oorti</i>	1	14
<i>planicaudus</i>	1	14
<i>pumilus</i>	5	14
<i>shebae</i>	2	14
<i>woodfordi</i>	2	14
<i>Luperosaurus</i>		
<i>joloensis</i>	1	14
<i>macgregori</i>	1	14
<i>Lygodactylus</i>		
<i>capensis</i>	4	14
<i>conraui</i>	2	14
<i>picturatus picturatus</i>	2	14
<i>Microgecko</i>		
<i>helenae</i>	4	14
<i>Millotissaurus</i>		
<i>mirabilis</i>	3	14
<i>Narudasia</i>		
<i>festiva</i>	3	14
<i>Pachydactylus</i>		
<i>bibronii bibronii</i>	5	14
<i>capensis capensis</i>	2	14
<i>geitje</i>	2	14
<i>Palmatogecko</i>		
<i>rangei</i>	4	14
<i>Paragehyra</i>		
<i>petiti</i>	1	14 ^b
<i>Perochirus</i>		
<i>guentheri</i>	4	14
<i>Phelsuma</i>		
<i>barbouri</i>	2	14
<i>cepediana</i>	4	13–14 (13.8)

TABLE 1—(Continued)

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
<i>laticauda</i>	2	14
<i>lineata</i> subsp.	2	14
<i>madagascariensis kochi</i>	2	14
<i>Phyllodactylus</i>		
<i>guentheri</i>	2	14
<i>homolepidurus homolepidurus</i>	3	14–15 (14.3)
<i>inexpectatus</i>	1	14
<i>julieni</i>	2	14
<i>lanei</i> subsp.	2	14
<i>marmoratus</i>	20	13–15 (13.9)
<i>palmatus</i>	1	14
<i>peringueyi</i>	1	15
<i>porphyreus porphyreus</i>	2	14
<i>tuberculosus tuberculosus</i>	4	14
<i>unctus</i>	2	14
<i>wolterstorffi</i>	1	14
<i>xanti nocticolus</i>	2	14
<i>Phyllopezus</i>		
<i>pollicaris pollicaris</i>	3	14
<i>pollicaris przewalskii</i>	4	14–15 (14.2)
<i>Pristurus</i>		
<i>carteri collaris</i>	2	14
<i>crucifer</i>	4	14
<i>flavipunctatus flavipunctatus</i>	6	14–16 (14.5)
<i>sokotranus</i>	2	14
<i>Pseudogekko</i>		
<i>compressicorpus</i>	1	14
<i>smaragdinus</i>	1	14
<i>Ptenopus</i>		
<i>garrulus</i>	2	15–17 (16.0)
<i>Ptychozoon</i>		
<i>kuhli</i>	2	14
<i>Ptyodactylus</i>		
<i>hasselquistii hasselquistii</i>	2	14
<i>hasselquistii ourdii</i>	2	14
<i>Quedenfeldtia</i>		
<i>trachyblepharus</i>	8	14
<i>Rhoptropella</i>		
<i>ocellata</i>	2	13–14 (13.5)
<i>Rhoptropus</i>		
<i>afer</i>	2	14
<i>bradfieldi bradfieldi</i>	2	14–15 (14.5)
<i>Saurodactylus</i>		
<i>fasciatus</i>	4	14
<i>mauritanicus brosetti</i>	8	14
<i>Tarentola</i>		
<i>americana</i>	2	14
<i>annularis</i>	2	14
<i>mauritanica mauritanica</i>	5	14
<i>neglecta</i>	2	14
<i>Teratolepis</i>		
<i>albofasciata</i>	6	14
<i>fasciata</i>	15	13–14 (13.9)

TABLE 1—(Continued)

	No. of Eyeballs	No. of Scleral Ossicles (Range and Mean)
<i>Thecadactylus rapicauda</i>	2	14
<i>Trachydactylus jolensis</i>	1	14 ^b
<i>Tropicolotes tripolitanus algericus</i>	2	14
<i>Uroplatus fimbriatus fimbriatus</i>	2	15
Gekkoninae (Group II)		
<i>Stenodactylus arabicus</i>	1	20
<i>doriae</i>	2	27–28 (27.5)
<i>grandiceps</i>	1	24
<i>khobarensis</i>	1	28
<i>major</i>	1	26
<i>petrii</i>	3	20–22 (21.0)
<i>pulcher</i>	1	24
<i>slevini</i>	1	26
<i>sthenodactylus sthenodactylus</i>	12	22–26 (24.0)
<i>sthenodactylus mauritanicus</i>	2	26–27 (26.5)
<i>Teratoscincus microlepis</i>	8	17–21 (19.4)
<i>scincus</i>	7	15–16 (15.3)
Sphaerodactylinae		
<i>Coleodactylus amazonicus</i>	4	12–14 (13.5)
<i>Gonatodes</i>		
<i>albogularis albogularis</i>	4	14
<i>albogularis fuscus</i>	4	14
<i>albogularis notatus</i>	2	14
<i>antillensis</i>	2	14
<i>atricucullaris</i>	6	14–15 (14.3)
<i>humeralis</i>	2	13–14 (13.5)
<i>vittatus vittatus</i>	4	14
<i>Lepidoblepharis microlepis</i>	4	13–14 (13.8)
<i>Pseudogonatodes barbouri</i>	2	14
<i>Sphaerodactylus</i>		
<i>argus henriquesi</i>	6	14
<i>cinereus</i>	4	14
<i>difficilis</i>	4	14–15 (14.3)
<i>goniorhynchus</i>	3	14
<i>inaguae</i>	4	14
<i>macrolepis macrolepis</i>	4	13–14 (13.5)
<i>mariguanae</i>	2	14
<i>mertensi</i>	2	14
<i>parkeri</i>	2	14–15 (14.5)
<i>torrei</i>	2	14–15 (14.5)

^a Includes *Coleonyx variegatus variegatus* and *Coleonyx variegatus sonoriensis*.^b Count approximate because of damaged eye.

found in both sexes of a species, although Wiedersheim (1876) reported them to be absent from females of *Phyllodactylus europaeus* (present in males). Brongersma (1934) has since corrected Wiedersheim's error. It appears that the sacs are, in general, much larger in males than in females. Noble and Bradley (1933) studied sections of these peculiar structures and found no evidence of glandular activity in the squamous epithelium lining the invagination. However, M. A. Smith (1933) stated that he found definite glandular cells in the wall of the sac but could not find any secretion in living or preserved specimens. The question of glandular activity in the cloacal sac is still unanswered. Noble and Bradley noted that the lining of the pocket is shed during the regular molting process and that the loose skin within the recess can be pulled out without any apparent discomfort to the animal. From these observations, the authors were led to the conclusion that the sac has no sensory function.

Noble and Bradley (1933) performed a few simple experiments on the sacs of living *Tarentola* which give some insight into their possible function. Sexual excitement appeared to cause the orifice of the sac to increase in diameter and the over-all depth of the sac to increase in length, producing a slight vacuum. Noble and Bradley inferred from this change in shape that the sacs act as stimulating organs that tend to quiet the female during copulation. M. A. Smith's (1933) conjecture that the sacs are homologous with the sex or scent gland of crocodiles and snakes has not been supported by any embryological or experimental data. Greenberg's (1943) study on the social behavior of *Coleonyx* provides the best evidence of their function. He stated that when the male rubs his cloacal spur across the cloaca of the female, the sacs of the male do not touch the female. When the spur becomes embedded in the cloaca of the female, the sac on the same side becomes obliterated by a folding of the skin, while the sac on the other side everts and becomes swollen. Greenberg suggested that the eversion of this sac acts to relieve pressure on the inactive hemipenis that remains swollen and sheathed. He further suggested that the other sac may provide freedom of rotation for the expanded base of the spur when the latter is

swung back by the final copulatory thrust of the male. These observations rule out the possible function ascribed to the sacs by Noble and Bradley (1933).

Cloacal bones are subcutaneous subcaudal elements found in almost all Gekkonoidea and in the xantusiid lizard genus *Xantusia*. The problem of homology has not been considered for these two widely different groups of lizards. The bones are restricted to males in the Gekkonoidea and are invariably found in close association with the cloacal sacs. There is either one pair or there are two pairs of these elements; the innermost is consistently present and borders the anterior, and generally the lateral, margins of the sac. It has been suggested that the inner element aids in enlarging the aperture of the sac. The absence of cloacal bones from females and the negative response to sexual stimulation, with regard to the size of the orifice and depth of the comparatively smaller sacs, may indicate that the sacs are without function in this sex. The outer pair of bones varies from small, simple, and platelike to large, elaborate (as in *Palmatogecko*), and strongly projecting beyond the surface of the tail. These outer elements when well developed definitely aid the males of some species in increasing the size of the cloaca of the female during copulation (Greenberg, 1943; Pope, 1956).

The presence of both cloacal sacs and associated bones appears to represent the primitive character-state in the Gekkonidae as inferred from their wide distribution within the family. The following observations strongly indicate that the loss of the cloacal bones is correlated with the loss of the closely associated sacs.

Cloacal sacs are present in all of the Eublepharinae and all of the Diplodactylinae. These invaginations are present in all gekkonine genera except the following: *Aristelliger*, *Lygodactylus* (variable?), *Millotisaurus*, *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus*. In addition, M. A. Smith (1933) stated that both *Phyllodactylus riebeckii* and *P. elisae* lack sacs and bones. *Ailuronyx* and *Perochirus* require re-examination before their condition can be stated with certainty. Postcloacal sacs are absent from all of the Sphaerodactylinae.

Two pairs of cloacal bones are present in all

of the Eublepharinae and one or two pairs in all of the Diplodactylinae. One or two pairs of bones are present in the Gekkoninae with the exception of the following genera: *Aristelliger*, *Lygodactylus* (variable?), *Millotisaurus*, *Narudasia*, *Pristurus*, *Quedenfeldtia*, and *Saurodactylus*. The following genera have not been examined: *Ailuronyx*, *Chondrodactylus*, *Luperosaurus*, *Ptenopus*, *Rhotropella*, and *Rhoptropus*. The bones are absent from all Sphaerodactylinae. It is interesting to note that all the genera in the Gekkoninae that lack sacs and bones are African (Madagascar included) in distribution with the exception of *Aristelliger* (West Indies and mainland of Central America). This correlation may indicate the section of the Gekkoninae that gave rise to the New World sphaerodactyline line. The absence of sacs and bones from the Gekkonidae is considered as having occurred only once, until evidence to the contrary is presented.

j-J. ANGULAR BONE

The lower jaw in primitive reptiles consisted of the following seven elements (Romer, 1956): dentary, coronoid, splenial, angular, prearticular, articular, and surangular. In the generalized lower jaw of the lizard all these elements are present, but the articular and prearticular are frequently fused. In addition, the surangular may fuse with the articular-prearticular complex, and the splenial and angular may be lost or fused to the remaining bones (fig. 6).

The dentary, coronoid, and articular-prearticular-surangular complex are consistently present in gekkonid lizards. The angular is present in the Eublepharinae in all species except *Coleonyx brevis* and *C. variegatus*. The angular is absent from the Diplodactylinae and Sphaerodactylinae. In the Gekkoninae, it is present only in *Teratoscincus*. The presence of the angular, the increase in scleral ossicle number, the absence of a calcified postcranial endolymphatic apparatus, if confirmed, and the single parietal (as exhibited by *Teratoscincus microlepis*) may indicate that *Teratoscincus* evolved directly from the eublepharine stock.

k-K. SPLENIAL BONE

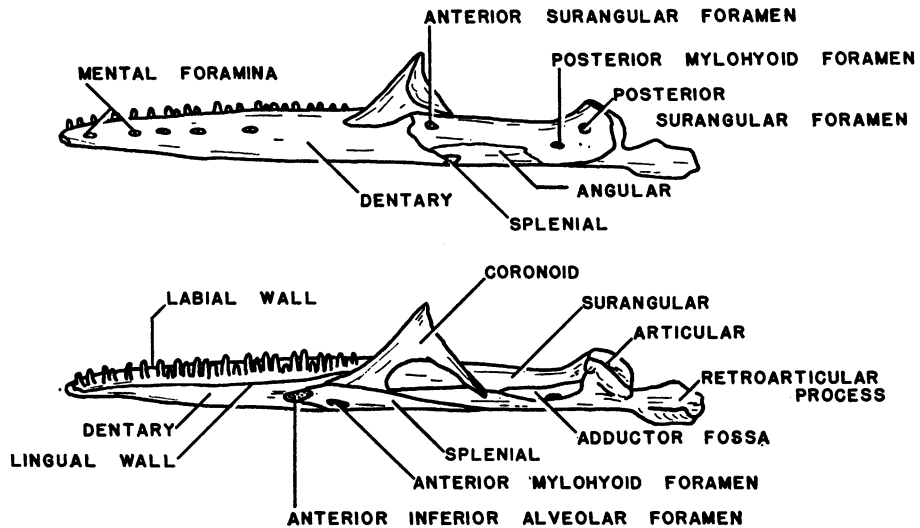
For introductory remarks on the splenial

bone, see character j-J (Angular Bone). The splenial is present in the Eublepharinae and Diplodactylinae. It is absent from only two gekkonine genera, *Pristurus* and *Ptyodactylus*, and from all of the Sphaerodactylinae. The loss of the splenial in *Pristurus* and *Ptyodactylus* probably occurred in parallel as inferred from their numerous morphological differences (compare the generic diagnoses given by Loveridge, 1947, pp. 71, 273, respectively). The many similarities between *Pristurus* and the Sphaerodactylinae besides the loss of the splenial, such as the (1) presence of diurnal or shade activity, (2) presence of sexual dichromatism, (3) presence of round pupil in life, (4) presence of an eyelid which is more or less distinctly formed by a circumorbital ring of tissue, (5) presence of simple, undilated digits, as in the more primitive sphaerodactyline *Gonatodes*, (6) small adult size, and (7) absence of preanal organs, may indicate a close relationship. It is for this reason that the loss of the splenial in *Pristurus* and the Sphaerodactylinae is not considered as having occurred in parallel (see table 2).

The most primitive lower-jaw condition in gekkonid lizards consists of the dentary, articular-prearticular-surangular, unreduced coronoid, splenial, and angular as exhibited by the Eublepharinae and *Teratoscincus*. The most advanced condition is represented by the Sphaerodactylinae in which only the dentary, articular-prearticular-surangular, and coronoid persist, with the last element being extremely reduced and in some species almost lost (fig. 6).

l-L. FRONTAL BONE

The frontal is the long, prominent, dermal, cranial element that usually forms the dorsal margin of the orbit. The descending lateral processes of the frontal meet ventrally and surround the olfactory lobes of the forebrain in the Gekkota. The frontal is almost invariably single in the Ascalabota, with the exception of the Xantusiidae. Some ardeosaurids exhibit the paired form as well, but that they do so is apparently owing to the preadult developmental stage of the fossil material (Hoffstetter, 1964). From the widespread occurrence of the single type of frontal throughout the Ascalabota, particularly among the more primitive gekkos, it is believed to be the



ORDER OF EVOLUTIONARY CHANGE

1. ANGULAR -	LOST
2. SPLENIAL -	LOST
3. CORONOID -	EXTREMELY REDUCED
4. ARTICULAR -	SLIGHTLY REDUCED
5. SURANGULAR -	UNMODIFIED
6. DENTARY -	UNMODIFIED

FIG. 6. Evolution of the lower jaw in the Gekkonidae. Lateral (above) and medial (below) views of the jaw of a hypothetical primitive gekko, with the bony elements and other points of reference indicated. The order of evolutionary change from primitive to advanced is indicated below the drawing.

primitive character-state in the Gekkonidae.

The frontal is single in all of the Eublepharinae, Diplodactylinae, and Sphaerodactylinae and in most of the Gekkoninae. The following gekkonine genera exhibit paired frontals: *Ailuronyx*, *Homopholis*, *Phelsuma*, *Rhoptropella*, *Saurodactylus*, and *Teratoscincus* (paired in *T. scincus*, fused in young and adult *T. microlepis*). The single frontal found in a few species of *Phelsuma* was probably derived from the paired state by an extensive filling in of bony material with age. The condition of the frontal in *Blaesodactylus* requires further study. *Teratoscincus* shows little rela-

tionship to the other gekkonine genera that possess paired frontals (see characters h-H, j-J, and r-R), and it seems likely that the condition has evolved at least twice within that subfamily. The paired frontals found in the Gekkoninae may be secondarily derived from the single form by arrested development and the retention of the embryonic condition.

m-M. NASAL BONES

The nasals are almost invariably moderately large, paired, dermal elements covering the dorsal surface of the nasal capsule in the Squamata. Paired nasals are considered

primitive in the Gekkonidae (fusion being advanced), as is inferred from the paired condition found in the ancestral ardeosaurids.

The nasals are paired in all of the Eublepharinae, Diplodactylinae, and Sphaerodactylinae. They are also paired in all Gekkoninae with the exception of adults of the following genera: *Ailuroonyx*, *Afroedura*, *Blaesodactylus*, *Cnemaspis* (*africana*, *boulengerii*, *kandiana*, *nigridius*, *q. quattuorseriata*, *siamensis*, and *wynadensis*; all other species listed in table 1 have paired nasals), *Cyrtodactylus* (*p. pelagicus*, *serpensinsula* and *vankampeni*; all other species listed in table 1 have paired nasals), *Ebenavia*, *Hemiphyllodactylus*, *Lepidodactylus*, *Lygodactylus*, *Perochirus*, *Phelsuma*, *Phyllodactylus* (*guentheri*, *marmorata*, and *p. porphyreus*), *Pseudogecko*, *Microgecko*, and *Uroplatus*.

Although the number of forms with fused nasals in the Gekkoninae is large, the condition in most genera appears to be associated with what are believed to be at least two natural groups within the subfamily. *Ailuroonyx*, *Afroedura*, *Blaesodactylus*, *Ebenavia*, *Lygodactylus*, *Phelsuma*, and *Uroplatus* form one group of relatively closely related genera restricted to the Ethiopian Region (with the exception of *Phelsuma andamanensis* of the Andaman Islands). The second group, consisting of *Hemiphyllodactylus*, *Lepidodactylus*, *Pseudogecko*, and possibly *Perochirus*, may be related and are essentially restricted to the eastern Oriental and the Oceanic regions. The former two assemblages of genera, if natural ones, seem to be unrelated and indicate that fusion of the nasals has occurred in parallel at least twice within the Gekkoninae. *Cnemaspis*, *Cyrtodactylus*, *Phyllodactylus*, and *Microgecko* which also have fused nasals cannot be placed satisfactorily in either group at this time nor do they form a very clearly defined assemblage of their own. The fact that *Cnemaspis*, *Cyrtodactylus*, and *Phyllodactylus* are interspecifically variable in this character suggests a case of multiple parallelism. Only for the convenience of coding are the four genera treated as one group.

n-N. PARIETAL BONE

In general, in the Squamata the parietal is initially paired, and during ontogeny it fuses to form a single element, normally shortly

after hatching. A single parietal is found in almost all adult non-gekkonid lizards and is considered the primitive lacertilian condition (Romer, 1956). It seems likely that the single parietal of the Ardeosauridae is directly ancestral to that condition found in primitive gekkonids.

The following remarks concerning the state of the parietal in gekkonid lizards apply only to adults, unless otherwise noted. The parietal is single in the Eublepharinae and paired in all of the Diplodactylinae and Sphaerodactylinae. It is paired in all gekkonine genera except *Perochirus* (only *guentheri* examined) and possibly *Pachydactylus b. bibronii*; in the latter species the extensive cranial ornamentation probably obscures the suture. The parietals were found to be fused in the largest adults of the sphaerodactyline *Gonatodes antillensis* and the gekkonine *Gehyra variegata*, *G. pilbara* (*vide* Mitchell, 1965), *Teratoscincus microlepis*, and some species of *Phyllodactylus* and *Phelsuma*. The fusion of the parietals in these forms appears to have been the result of the filling in of bony material with age.

It seems that the paired condition of the parietals, found in the majority of gekkos, has been derived from the primitive fused gekkonid type represented by the Eublepharinae and the ancestral Ardeosauridae. The paired condition may be a neotenic feature of the Gekkonidae (Stephenson, 1960). The single parietal of *Perochirus* is considered to be a reversion to the primitive form and therefore is treated as a specialized character-state in the Gekkoninae (see table 2).

o-O. AMPHICOELOUS OR PROCOELOUS PRESACRAL VERTEBRAE

All Squamata have procoelous presacral vertebrae, with the exception of many gekkonid lizards. The occurrence of both procoely and amphicoely has been used by most herpetologists as a major systematic character within the Gekkonidae. Underwood (1954) stated that the amphicoelous condition, found in most gekkos, was secondarily derived from a procoelous type, although he was later dissuaded from this viewpoint (Underwood, 1955) by the discoveries of supposedly definitive amphicoelous Triassic

lizards. It now appears that this group of Mesozoic reptiles (*Kuehneosaurus* Robinson, 1962) actually formed a separate radiation and were not directly ancestral to lizards as Underwood and others were led to believe.

I agree with Underwood (1954) and Romer (1956) in considering procoely the primitive presacral vertebral form in lizards. The fact that the Ardeosaurinae have procoelous vertebrae supports this thesis for gekkonid lizards. I have not found the arguments presented by Camp (1923) and Holder (1960) to be of sufficient weight to consider amphicoely the primitive condition.

All of the Eublepharinae are procoelous. In the Diplodactylinae typical amphicoely predominates except for the following genera: *Carphodactylus*, *Crenadactylus*, *Diplodactylus*, *Oedura*, and *Phyllurus*. In these diplodactyline genera there is a tendency toward procoely; however, no specimen examined attained the typical saurian form. All Gekkoninae are amphicoelous with the single exception of *Ebenavia* which exhibits a typical procoelous condition. In the Sphaerodactylinae only *Gonatodes* is amphicoelous; all other genera are procoelous.

It appears that the primitive gekkonid vertebral type was procoelous, as exhibited today by the Eublepharinae and derived from the Jurassic Ardeosaurinae. On the basis of the development of procoelous vertebrae, as discussed by Romer (1956, p. 255) and Holder (1960, pp. 302-7), it seems likely that the amphicoelous condition found in the majority of the gekkos could have been derived from the procoelous type by arrested development and retention of the embryonic form. The tendency toward procoely, as exhibited by some diplodactyline genera, could have evolved secondarily by suppression of the neotenic process, or it might simply be a reflection of the primitive genetic background of the subfamily. The gekkonine genus *Ebenavia* probably followed the former course.

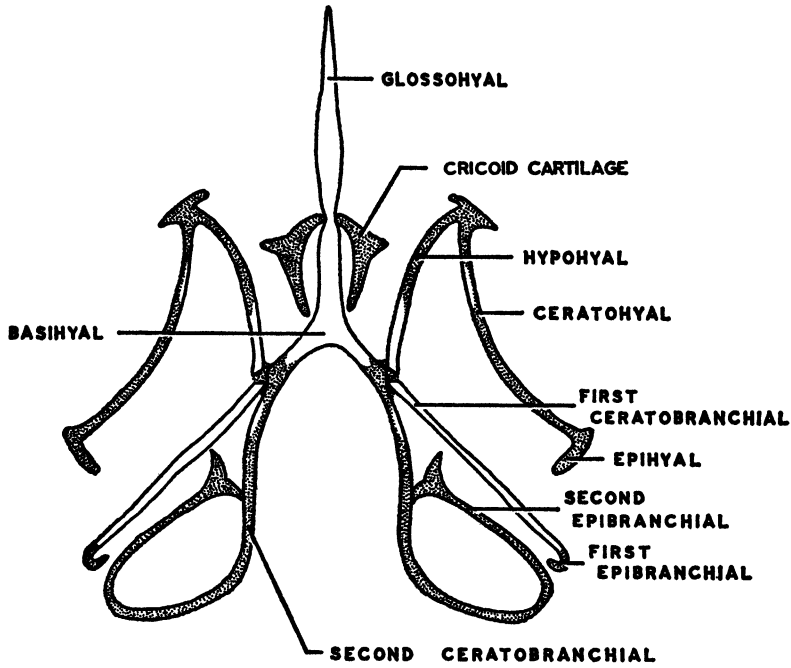
There appears to be little doubt that the amphicoelous *Gonatodes* is the most primitive member of the Sphaerodactylinae; e.g., it possesses (1) a large, unreduced coronoid, (2) a large squamosal, (3) a large, unreduced, paroccipital process of the opisthotic, and (4) a primitive type of digit (Noble, 1921;

Parker, 1926). The other sphaerodactyline genera, which are all procoelous, have probably evolved from a *Gonatodes*-like ancestor. Noble (1921) was the first to recognize this morphogenetic sequence in the Sphaerodactylinae. Noble's observations strongly support the view that procoely has developed secondarily in the Sphaerodactylinae.

p-P*. HYOID ARCH

The reptilian hyoid apparatus is an extremely complex structure which was derived from the ancestral amphibian hyoid arch and two posterior visceral arches. The apparatus lies in the floor of the mouth and pharynx and is closely associated with the musculature of those regions. The apparatus functions in supporting and moving the tongue and larynx. Three complete (unbroken) arches are considered the primitive saurian condition (Romer, 1956). The hyoid nomenclature used here follows that of Kluge (1962).

In the Eublepharinae, the hyoid cornu, the large, winglike projection at the hypohyal-ceratohyal union, is constant in shape and similar to that shown for *Coleonyx* (Kluge, 1962). Apparently the inner proximal ceratohyal projection is absent from all genera. The Diplodactylinae exhibit a large and variably shaped hyoid cornu. The inner proximal ceratohyal projection was found in only the following genera: *Carphodactylus*, *Naultinus*, *Nephrurus*, and *Phyllurus*. The gekkonine hyoid cornu varies in shape and size and is absent only from *Tropicolotes*. The hypohyal-ceratohyal union is very tenuous in the latter genus. The inner proximal ceratohyal projection is present in or absent from the Gekkoninae. In the Sphaerodactylinae, the hyoid cornu is relatively large in *Gonatodes* and *Lepidoblepharis*, slightly less developed in *Sphaerodactylus*, almost completely absent from *Pseudogonatodes*, and entirely lacking in *Coleodactylus*. The hypohyal-ceratohyal union is interrupted in the last-mentioned genus. The hyoid arch of the gekkonine genus *Tropicolotes* has gone slightly beyond the evolutionary state reached by *Pseudogonatodes* and approaches that of *Coleodactylus* (fig. 7). The discontinuation of the hypohyal-ceratohyal union is almost certainly associated with the loss of the hyoid cornu. The evolu-



ORDER OF EVOLUTIONARY CHANGE

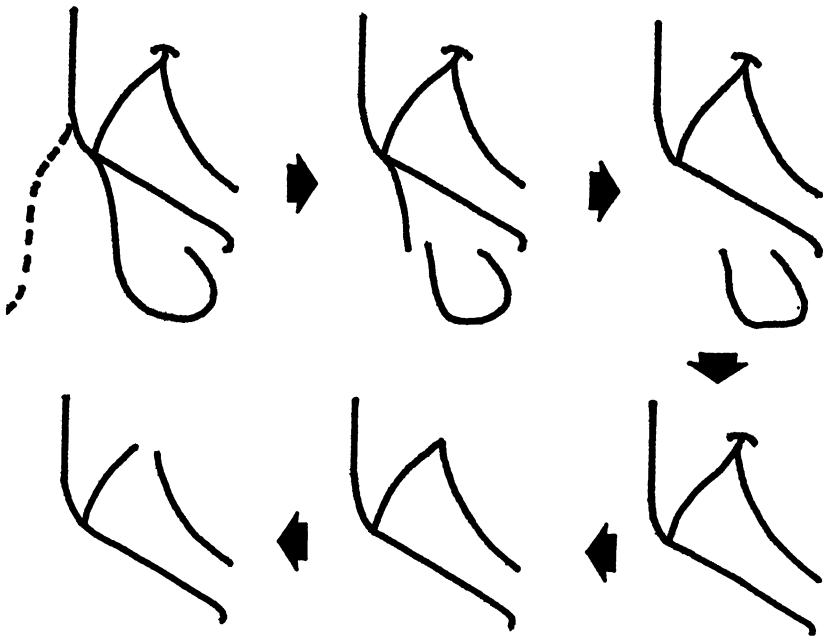


FIG. 7. Evolution of the branchial apparatus in the Gekkonidae. Ventral view of the primitive branchial apparatus of *Coleonyx v. variegatus*. The order of evolutionary change from primitive to advanced can be visualized from the schematic diagrams by following the course of the arrows (only the right side of the apparatus is shown).

tionary trend toward the loss of the hyoid cornu and the interruption of the hypohyal-ceratohyal union has probably been established independently in the Gekkoninae and Sphaerodactylinae; the conditions in *Tropicolotes* and *Pseudogonatodes* are treated as the same character-state but as having evolved in parallel. The inner proximal ceratohyal projection is present in *Gonatodes*, *Lepidoblepharis*, and *Sphaerodactylus*. The loss of this projection in *Pseudogonatodes* and *Coleodactylus* appears to be associated with the trend toward a discontinuous hyoid arch. It seems likely that the inner proximal projection of the ceratohyal has been lost independently in each of the four subfamilies. It is also possible that this process has evolved more than once within the Gekkonidae.

q-Q****. SECOND VISCERAL ARCH

For introductory remarks on the hyoid apparatus, see character p-P* (Hyoid Arch). In the Eublepharinae, *Coleonyx* exhibits three complete visceral arches which represent a unique condition in modern lizards (Kluge, 1962). The second visceral arch is separated in all other eublepharine genera, but the ceratobranchial and epibranchial parts form an extensive secondary zone of unfused contact. The second visceral arch is invariably discontinuous in the Diplodactylinae, and the long ceratobranchial and epibranchial parts are normally separated by moderate to large distances, with the exception of *Rhynchoedura*. The ceratobranchial and epibranchial overlap in the latter genus but do not come into contact. Stephenson and Stephenson (1956) stated that *Naultinus* had three complete arches. My material of this genus indicates an interruption in the second visceral arch. The ceratobranchial is moderately long to very long in all diplodactylina genera. The second visceral arch appears to be consistently broken in the Gekkoninae. The second ceratobranchial was completely absent from 60 per cent of the genera examined (the advanced condition), and in the remaining 40 per cent it ranged from being moderately long to being very long. The second epibranchial was present in all genera with the exception of *Pristurus*. In all of the Sphaerodactylinae, the second visceral arch

is interrupted. The ends of the long ceratobranchial and epibranchial approach each other very closely (in one specimen of *Sphaerodactylus parkeri* they overlapped, and in one specimen of *Gonatodes v. vittatus* they secondarily fused; apparently both specimens were abnormal). The second epibranchial is present in all genera except *Coleodactylus*. The loss of the epibranchial appears to be correlated with shortening and the ultimate loss of the paroccipital process of the opisthotic in this genus, as well as in the gekkonine genus *Pristurus* (fig. 7). The loss of the epibranchial in the most advanced sphaerodactylina genus *Coleodactylus* and in *Pristurus* is interpreted as having occurred in parallel.

The following evolutionary trends in the morphology of the hyoid apparatus of gekkonid lizards are readily perceived (fig. 7). Primitively, three complete arches were present. Departures from the primitive condition involve successive discontinuities in the second visceral arch and then in the hyoid arch. After the second visceral arch is interrupted, the ceratobranchial is frequently lost. The second epibranchial is usually retained; however, it is reduced, and in some genera it is lost along with the reduction and ultimate loss of the paroccipital process of the opisthotic.

r-R. SQUAMOSAL BONE

For introductory remarks on the squamosal bone, see character g-G (Supratemporal Bone). The squamosal is consistently present in all Eublepharinae and Diplodactylinae. In the Gekkoninae, the squamosal is absent only from *Lygodactylus*, *Saurodactylus mauritanicus brosetti* (although present in *S. fasciatus*), and *Teratoscincus*. The squamosal is present in all Sphaerodactylinae except *Coleodactylus*.

The loss of the squamosal appears to be correlated with the reduction of the paroccipital process of the opisthotic except in *Teratoscincus*. As the paroccipital process shortens, and the squamosal is lost, the quadrate moves medially under the cranial complex and eventually articulates with the prootic. In *Teratoscincus* the quadrate articulates loosely with the large paroccipital process. It appears that the squamosal has

been lost independently in the Gekkoninae and the Sphaerodactylinae (i.e., *Coleodactylus* is the most highly evolved sphaerodactylinae and does not share any other diagnostic features with more generalized Gekkoninae). Within the Gekkoninae there is some morphological similarity between *Lygodactylus* and *Saurodactylus*; however, *Teratoscincus* appears to be totally unrelated (see other character discussions). The loss of the squamosal within the Gekkoninae is therefore inferred as having occurred in parallel (fig. 3).

EVOLUTION OF THE SUBFAMILIES

The coding and weighting of the characters discussed above are necessary preliminaries to the delimitation of natural assemblages of genera by the method used here and the calculation of advancement (divergence) indexes for the recognized taxa (tables 2 and 3). The following list indicates the letter symbols and number of character-states of each character, the primitive or advanced condition of each state and its numerical weight, and suggested parallelisms.

- Character a-A: True eyelids or spectacle (2 character-states)
 a. True eyelids present (primitive); weight 1
 A. Spectacle present (advanced); weight 2
- Character b-B: Development of premaxillary bone (2 character-states)
 b. From two centers of ossification (primitive); weight 1
 B. From one center of ossification (advanced); weight 2
- Character c-C: Postcranial endolymphatic apparatus (2 character-states)
 c. Calcified sac absent (primitive); weight 1
 C. Calcified sac present (advanced); weight 2
- Character d-D: Distribution of escutcheon scales (2 character-states)
 d. Absent (primitive); weight 1
 D. Present (advanced); weight 2
- Character e-E: Ability to vocalize (2 character-states)
 e. Present (primitive); weight 1
 E. Absent (advanced); weight 2
- Character f-F: Number of eggs laid (2 character-states)
 f. Two (primitive); weight 1
 F. One (advanced); weight 2
- Character g-G: Supratemporal bone (2 character-states)
 g. Present (primitive); weight 1
 G. Absent (advanced); weight 2
- Character h-H: Number of scleral ossicles per eyeball (2 character-states)
 h. Significantly more than 14 (primitive); weight 1
 H. Approximately 14 (advanced); weight 2
- Character i-I: Cloacal sacs and bones (2 character-states)
 i. Present (primitive); weight 1
 I. Absent (advanced); weight 2
- Character j-J: Angular bone (2 character-states)
 j. Present (primitive); weight 1
 J. Absent (advanced); weight 2
- Character k-K: Splenial bone (2 character-states)
 k. Present (primitive); weight 1
 K. Absent (advanced); weight 2
K. Absent (advanced—independent of K); weight 2
- Character l-L: Frontal bone (2 character-states)
 l. Single (primitive); weight 1
 L. Paired (advanced); weight 2
L. Paired (advanced—independent of L); weight 2
- Character m-M: Nasal bones (2 character-states)
 m. Paired (primitive); weight 1
 M. Fused (advanced); weight 2
M. Fused (advanced—independent of M and M); weight 2
M. Fused (advanced—independent of M and M); weight 2
- Character n-N: Parietal bone (2 character-states)
 n. Single (primitive); weight 1
 N. Paired (advanced); weight 2
n. Single (advanced—reversion to primitive condition); weight 3
- Character o-O: Type of presacral vertebrae (2 character-states)
 o. Procoelous (primitive); weight 1
 O. Amphicoelous (advanced); weight 2
o. Procoelous (advanced—reversion to primitive condition, independent of o); weight 3
o. Procoelous (advanced—reversion to primitive condition, independent of o); weight 3
- Character p-P*: Hyoid arch (3 character-states)
 p. Hyoid cornu large, hypohyal-ceratohyal union not tenuous (primitive); weight 1
 P. Hyoid cornu small, hypohyal-ceratohyal union tenuous (advanced); weight 2
 P*. Hyoid cornu absent, hypohyal-ceratohyal union broken (more advanced than P); weight 3
P. Hyoid cornu small, hypohyal-ceratohyal union tenuous (advanced—independent of P); weight 2
- Character q-Q****: Second visceral arch (5 character-states)
 q. Ceratobranchial-epibranchial union continuous (primitive); weight 1
 Q. Ceratobranchial-epibranchial union broken,

TABLE 2
DISTRIBUTION OF CHARACTERS

Subfamilies	Characters																	
	a-A	b-B	c-C	d-D	e-E	f-F	g-G	h-H	i-I	j-J	k-K	l-L	m-M	n-N	o-O	p-P*	q-Q****	r-R
Eublepharinae	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o	p	q	r
					G		G		J								Q	
Diplodactylinae	A	b	c	d	e	f	G	h	i	J	k	l	m	N	O	P	Q	r
													m				Q*	r
Gekkoninae	A	B	C	d	e	f	G	h	i	j	k	l	M	n	o	P	Q**	R
							H	I	J	K	L	M	M	N	O	P	Q****	R
											K	L	M					
Sphaerodactylinae	A	B	C	D	E	F	G	H	I	J	K	l	m	N	O	P	Q	r
																	Q***	R
																P*		

elements overlap and remain in close association (advanced); weight 2

Q*. Ceratobranchial-epibranchial union broken and elements widely separated (more advanced than Q); weight 3

Q**. Ceratobranchial lost, epibranchial present (more advanced than Q*); weight 4

Q***. Ceratobranchial present, epibranchial lost (more advanced than Q*—independent of Q**); weight 4

Q****. Ceratobranchial lost, epibranchial lost (more advanced than Q** and Q***); weight 5

Q. Ceratobranchial-epibranchial union broken, elements overlap and remain in close association (advanced—independent of Q); weight 2

Character r-R: Squamosal bone (2 character-states)

r. Present (primitive); weight 1

R. Absent (advanced); weight 2

R. Absent (advanced—independent of R and R); weight 2

R. Absent (advanced—independent of R and R); weight 2

I have grouped the 82 genera that were examined in this study into four subfamilies (Eublepharinae, Diplodactylinae, Gekkoninae, and Sphaerodactylinae) on the basis of the greatest number of shared or unshared characters and least number of parallelisms (table 2; fig. 8). The use of these criteria with multiple characters, both internal and external, and the fact that the taxonomic products are consistent with present zoogeographical concepts strongly suggest that the recognized subfamilies are natural ones. The distribution of the character-states in each subfamily (reduced from a generic table for the sake of brevity) is easily visualized when table 2 is read horizontally; when table 2 is read vertically the evolutionary trend or trends of each character are indicated relative to the taxa. The genera that compose the subfamilies are listed below, following an expanded definition of the higher taxa and a brief description of their geographical range.

SUBFAMILY EUBLEPHARINAE

DIAGNOSIS: True eyelids present, spectacle absent; premaxilla developing from two centers of ossification, paired condition persisting in some adults; calcified endolymphatic sacs in postcranial region absent; preanal organs almost invariably present, escutcheon

scales absent; voice present; two eggs laid; supratemporal present or absent; scleral ossicles 13 to 25 (mean 16.7; average deviation of the means of the genera 2.7); cloacal sacs and two pairs of cloacal bones present; angular rarely absent; splenial present; frontal single; nasals paired; parietal single; vertebrae procoelous; hyoid cornu present; inner proximal ceratohyal projection absent; second visceral arch continuous or interrupted; if second visceral arch is interrupted, ceratobranchial and epibranchial forming extensive zone of unfused contact; squamosal present.

RANGE: A discontinuous distribution; two genera restricted to the Oriental Region, two to the Ethiopian Region, and one to southern North America and Central America (map 1).

GENERA EXAMINED: *Aeluroscalabotes* Boulenger; *Coleonyx* Gray; *Eublepharis* Gray; *Hemitheconyx* Stejneger; *Holodactylus* Boettger.

SUBFAMILY DIPLODACTYLINAE

DIAGNOSIS: True eyelids absent, spectacle present; premaxilla developing from two centers of ossification, paired condition persisting in some adults; calcified endolymphatic sacs in postcranial region absent; preanal organs generally present, escutcheon scales absent; voice present; two eggs laid, or bearing living young; supratemporal absent; scleral ossicles 21 to 40 (mean 31.9; average deviation of the means of the genera 3.8); cloacal sacs and one or two pairs of cloacal bones present; angular absent; splenial present; frontal single; nasals paired; parietal paired; vertebrae generally amphicoelous, some tendency toward procoely; hyoid cornu present; inner proximal ceratohyal projection rarely present; second visceral arch interrupted; ceratobranchial long, normally separated from epibranchial by moderate to large distance; squamosal present.

RANGE: Restricted to Australia (excluding Tasmania), New Caledonia and the Loyalty Islands, and New Zealand (map 1).

GENERA EXAMINED: *Bavayia* Roux; *Carpodactylus* Günther; *Crenadactylus* Dixon and Kluge; *Diplodactylus* Gray; *Eurydactylodes* Wermuth; *Heteropholis* Fischer; *Hoplodactylus* Fitzinger; *Naultinus* Gray; *Nephrurus* Günther; *Oedura* Gray; *Phyllurus*

Schinz; *Pseudothecadactylus* Brongersma; *Rhacodactylus* Fitzinger; *Rhynchoedura* Günther.

SUBFAMILY GEKKONINAE

DIAGNOSIS: True eyelids absent, spectacle present; premaxilla developing from single center of ossification, paired condition absent from adults; calcified endolymphatic sacs present in postcranial region; preanal organs either present or absent, escutcheon scales absent; voice present; two eggs laid; supratemporal absent; scleral ossicles in Group I 13 to 17 (mean 14.0; average deviation of the means of the genera 0.2), in Group II 15 to 28 (mean 21.7; average deviation of the means of the genera 3.4); cloacal sacs and bones (either one or two pairs) variable, present in 86 per cent, absent from 14 per cent; angular almost invariably absent; splenial rarely absent; frontal variable, single in 87 per cent, paired in 13 per cent; nasals variable, paired in 72 per cent, single in 28 per cent; parietal paired (single exception); vertebrae amphicoelous (single exception); hyoid cornu almost invariably present; inner proximal ceratohyal projection either present or absent; second visceral arch interrupted; ceratobranchial variably present in 40 per cent, absent from 60 per cent; ceratobranchial, if present, separated from epibranchial by moderate to large distance; epibranchial present (single exception); squamosal rarely absent.

RANGE: Circumglobal; New World between latitude 48° S. and latitude 35° N.; Old World between latitude 40° S. and latitude 50° N. (map 1). Found on all major land masses and almost all oceanic islands.

GENERA EXAMINED: *Afroedura* Loveridge; *Agamura* Blanford; *Ailuronyx* Fitzinger; *Al-sophylax* Fitzinger; *Aristelliger* Cope; *Blaesodactylus* Boettger; *Bogertia* Loveridge; *Briba* Amaral; *Bunopus* Blanford; *Calodactylodes* Strand; *Chondrodactylus* Peters; *Cnemaspis* Strauch; *Colopus* Peters; *Cosymbotus* Fitzinger; *Crossobamon* Boettger; *Cyrtodactylus* Gray; *Davidogecko* Smith; *Ebenavia* Boettger; *Geckolepis* Grandidier; *Geckonia* Mocquard; *Gehyra* Gray; *Gekko* Laurenti; *Gymnodactylus* Spix; *Hemidactylus* Oken; *Hemiphyllo-dactylus* Bleeker; *Heteronotia* Wermuth; *Homonota* Gray; *Homopholis* Boul-

enger; *Lepidodactylus* Fitzinger; *Luperosaurus* Gray; *Lygodactylus* Gray; *Microgecko* Nikolsky; *Millotisaurus* Pasteur; *Narudasia* Methuen and Hewitt; *Pachydactylus* Wiegmann; *Palmatogecko* Anderson; *Paragehyra* Angel; *Perochirus* Boulenger; *Phelsuma* Gray; *Phyllodactylus* Gray; *Phyllopezus* Peters; *Pristurus* Rüppell; *Pseudogekko* Taylor; *Ptenopus* Gray; *Ptychozoon* Kuhl; *Ptyodactylus* Goldfuss; *Quedenfeldtia* Boettger; *Rhoptropella* Hewitt; *Rhoptropus* Peters; *Saurodactylus* Fitzinger; *Stenodactylus* Fitzinger; *Tarentola* Gray; *Teratolepis* Günther; *Teratoscincus* Strauch; *Thecadactylus* Goldfuss; *Trachydactylus* Haas and Battersby; *Tropicolotes* Peters; *Uroplatus* Duméril.

SUBFAMILY SPHAERODACTYLINAE

DIAGNOSIS: True eyelids absent, spectacle present; premaxilla developing from single center of ossification, paired condition absent from adults; calcified endolymphatic sacs present in postcranial region; preanal organs absent, escutcheon scales present; voice absent; single egg laid; supratemporal absent; scleral ossicles 12 to 15 (mean 14.0; average deviation of the means of the genera 0.1); cloacal sacs and bones absent; angular absent; splenial absent; frontal single; nasals paired; vertebrae generally procoelous; hyoid cornu variable, rarely absent; hyoid arch almost invariably continuous; inner proximal ceratohyal projection variable, either present or absent; second visceral arch interrupted; ceratobranchial long, normally separated from epibranchial by small distance; second epibranchial rarely absent; squamosal rarely absent.

RANGE: Confined to New World tropics, between latitude 22° S. and latitude 26° N. Known from both the Cocos and Galapagos Islands in the Pacific and generally present throughout the West Indies (map 1).

GENERA EXAMINED: *Coleodactylus* Parker; *Gonatodes* Fitzinger; *Lepidoblepharis* Peracca; *Pseudogonatodes* Ruthven; *Sphaerodactylus* Wagler.

In table 3, the numerical values that indicate the primitive or advanced states replace letter symbols. The relative degree of divergence (advancement index) for each family is the total of their numerical values (last column, table 3). Fractions of whole numbers

TABLE 3
CALCULATION OF ADVANCEMENT INDEX

Subfamilies	Characters																Total A.I.		
	a-A	b-B	c-C	d-D	e-E	f-F	g-G	h-H	i-I	j-J	k-K	l-L	m-M	n-N	o-O	p-P*		q-Q****	r-R
Eublepharinae	1	1	1	1	1	1	0.53	1	1	0.90	1	1	1	1	1	1	0.20	1	19.36
							0.93			0.20							1.60		
Diplodactylinae	2	1	1	1	1	1	2	1	1	1	1	1	1	2	2	1	0.14	1	24.93
																	2.79		
Gekkoninae	2	2	2	1	1	1	2	0.04	0.86	0.02	0.98	0.87	0.27	0.06	0.06	0.98	1.18	0.95	29.31
							1.93	0.28	1.96		0.04	0.20	0.15	1.96	1.96	0.04	2.35	0.06	
											0.04	0.06	0.15				0.10	0.04	
													0.15						
Sphaerodactylinae	2	2	2	2	2	2	2	2	2	2	2	1	1	2	2	0.60	1.60	0.80	34.00
																0.40	0.80	0.40	
																0.60	0.60	0.40	

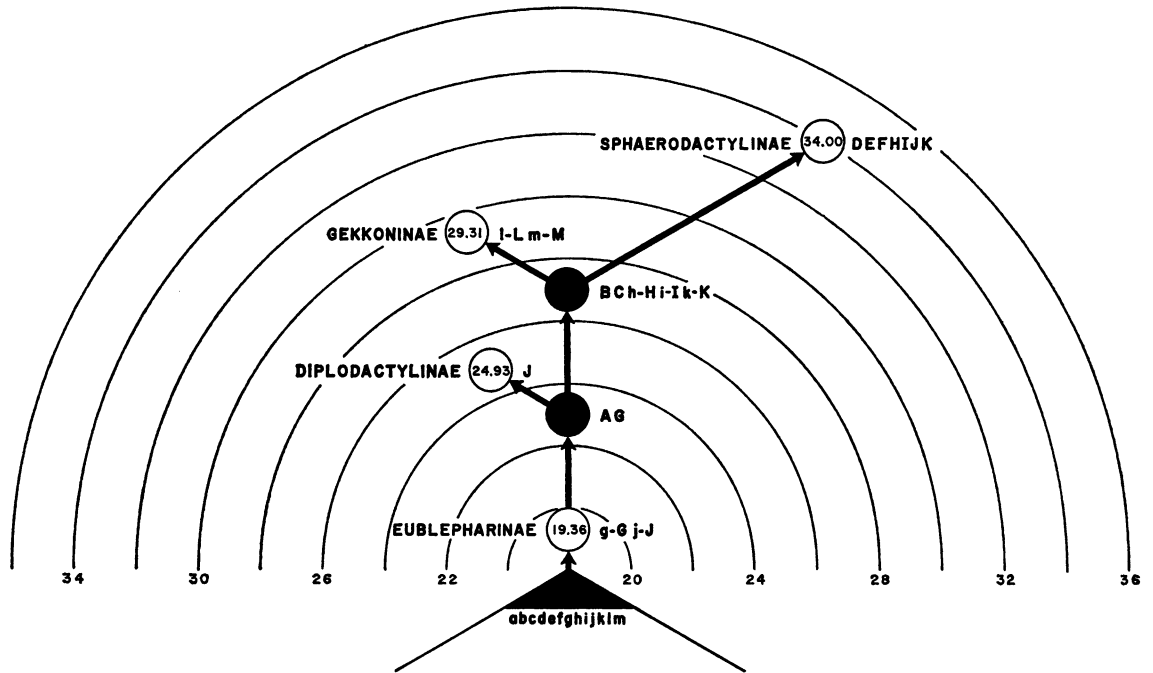


FIG. 8. Phylogeny of the Gekkonidae expressed in the form of a dendrogram which is superimposed on a background of advancement indexes. Open circles indicate the presently recognized subfamilies, Eublepharinae, Diplodactylinae, Gekkoninae, and Sphaerodactylinae; closed circles suggest hypothetical intermediate taxa. Numbers refer to degrees of advancement from the primitive number based, on 18 characters. The letters (a to m) correspond to the characters as they are coded on pages 39–41. Once the character-state changes (e.g., from a to A, or from g to g-G), the reader can assume that all derived taxa (hypothetical or extant) also exhibit that state.

were used in cases in which there was more than one character-state within a taxon. The fractions were determined by dividing the numerical value by the percentage of the total number of genera examined (and species if intragenerically variable) that exhibited that particular state.

The phylogenetic relationships are expressed in the form of a dendrogram (fig. 8) which is superimposed on a background of advancement indexes similar to that used by W. H. Wagner, Jr., and his students at the University of Michigan (Hardin, 1957; Wagner, 1961; Scora, 1966; see Lellinger, MS, for critical review of the method). Those characters that exhibit intersubfamilial parallelisms (n-N to r-R; table 2) were not used in the construction of the dendrogram, but the numerical values for all 18 characters (table 3) were employed in determining the advancement index of each subfamily.

The generic assemblages are considered to

be of equal taxonomic rank (subfamilies) because of the nearly uniform increase in the total advancement index from group to group (table 3): advancement index, 5.57 between the Eublepharinae and Diplodactylinae, 4.38 between the Diplodactylinae and Gekkoninae, and 4.69 between the Gekkoninae and Sphaerodactylinae.

ZOOGEOGRAPHICAL HISTORY OF THE SUBFAMILIES

I can comment on the fundamental zoogeographical features of the Gekkonidae, using as a basis for the discussion our knowledge of the present geographical distribution of the subfamilies, their proposed relationships, and their probable course of evolution (maps 1, 2; fig. 8). A general understanding of the zoogeography of the family is a necessary preliminary to more detailed studies on the subfamilies which are in preparation.

The Gekkonidae almost certainly evolved

from the basic Gekkota stock some time in the Mesozoic, probably during Upper Jurassic-Lower Cretaceous. Jurassic-Cretaceous age seems appropriate on the basis of the relationships of the Gekkonidae to the neo-Jurassic Ardeosauridae and the time probably required for the Gekkonidae to have reached the morphological stage of evolution exhibited by the early and middle Tertiary fossils known from France, Morocco, and the United States (Hoffstetter, 1946, 1961; Estes, 1963).

The circumglobal disjunct distribution of the Eublepharinae (all genera are allopatric; map 1) and the large number of primitive characters retained by this subfamily (see tables 2 and 3; the divergence index is only 1.36 from the hypothetical primitive form on the basis of 18 characters) suggest that it is represented today by a group of primitive relict genera. The genus *Aeluroscalabotes* is restricted to Malaya, southern Thailand, Sumatra, Borneo, and the Soela Islands (probably Sanana). It is very distinct morphologically from all related genera, and, on the basis of the following skeletal features, it appears to be the most primitive genus in the subfamily and therefore in the entire family: the splenial and angular in the lower jaw and the squamosal and supra-temporal in the temporal region are invariably present, and the scleral ossicle number is in the mid-twenties (23 to 25). The massiveness of the platelike interclavicle and clavicles, which are almost invariably imperforate, also strongly suggests a primitive form (Camp, 1923, pp. 366-369). Almost without exception, *Aeluroscalabotes* has been found at night in tropical forests on vegetation (from ground level to 10 feet high) usually associated with watercourses (Taylor, 1963; Robert F. Inger and F. Wayne King, personal communications). All other genera in this primitive subfamily inhabit more arid areas and therefore more recently evolved floral habitats, because the early period of gekkonid evolution took place in association with the Late Mesozoic and Tropical Tertiary Geofloras (Axelrod, 1959, 1960). From the above evidence it appears that southeast Asia may have been the place of origin and early evolution of the Eublepharinae and possibly of all gekkonid lizards. The peculiar geographical

distribution of the allopatric species of *Eublepharis* (see following discussion for details) and the fact that this genus appears to be more closely related to *Aeluroscalabotes* than does any other (see individual discussions of subfamilial diagnostic characters) also suggest southeast Asia as the center of early gekkonid evolution.

Additional support for southeast Asia as a place of origin of gekkonid lizards can be taken from the Diplodactylinae. This relatively primitive subfamily is restricted to the Australian Region (Kluge, MS). The fact that the most likely course of entry into the region was via the Indo-Australian archipelago and the rather well-established relationships with the Eublepharinae also indicate southeast Asia as the place of origin for the family.

The possibility of an eastward dispersal of the Eublepharinae in the direction of the Australian land mass by way of the Indo-Australian archipelago is strongly suggested by the geographical proximity of *Aeluroscalabotes* to that region (a subspecies, *A. dorsalis multituberculatus*, is known from the Soela Islands, probably Sanana, only 350 miles west of New Guinea). If the Eublepharinae migrated to the New Guinea-Australian land mass (Termier and Termier, 1952), possibly they were replaced by the major diplodactyline radiation that centered in that region (Kluge, MS).

The arboreal habit of the straight-toed *Aeluroscalabotes*, in contrast to its straight-toed terrestrial subfamilial counterparts, can be interpreted either as a specialization or as a vestige of the primitive gekkonid mode of life. The digits of *Aeluroscalabotes* are short, straight, and thick and do not appear to be supplied with specialized microscopic clinging structures. The only digital feature that might be associated with arboreal life is the nearly zygodactylous position of the digits and the enlarged palmar scales (Rooij, 1915, p. 27, fig. 16). The body of *Aeluroscalabotes* is long and relatively slender, and the tail is prehensile (F. Wayne King, personal communication), as is typical of many arboreal lizards, but the limbs are relatively short and stout (round in cross section) and do not appear to be well suited for climbing, particularly in tropical vegetation. Their slow,

deliberate movements are similar to those of chameleons. The contrasting arboreal and non-arboreal features of *Aeluroscalabotes* may be indicative of the generalized (primitive) condition of the family.

The genus *Eublepharis* appears to be much more closely related to *Aeluroscalabotes* than do the other eublepharine genera (see individual discussions of the subfamilial diagnostic characters, and Kluge, 1962) and probably evolved from an *Aeluroscalabotes*-like stock in southeast Asia. This phase of eublepharine evolution probably occurred in the late Cretaceous, but convincing evidence in support of this point of view is lacking for the most part. As discussed below, the early Tertiary dispersal of a *Coleonyx*-like form to the New World necessitates a pre-Tertiary origin of *Eublepharis*. Doubtless, the ancestral *Eublepharis* had a much wider geographical range in the past, as can be inferred from the present-day disjunct distribution of the genus (southwestern Asia, Norway Islands, Gulf of Tongkin, Hainan, and the Riu Kiu Islands). From the widespread ancestral *Eublepharis* group it appears that there were at least two separate lines of evolution: (1) a New World group, now represented by *Coleonyx*, and (2) an African radiation represented by two genera, *Holodactylus* and *Hemitheconyx*. The single New World eublepharine genus *Coleonyx* almost certainly originated from a *Eublepharis*-like ancestor (Kluge, 1962) and probably arrived in North America by way of the Bering land bridge through the continuous Paleocene Subtropical floral belt (Axelrod, 1952, 1958). The present distribution of *Coleonyx* (Klauber, 1945) suggests that the genus did not enter South America. This interpretation is consistent with the fact that North and South America were isolated by seaways of varying breadth throughout almost all of the Tertiary (Simpson, 1953). *Coleonyx* is represented today by two very different groups of species (Kluge, 1962): (1) a northern group consisting of *variegatus* (including *fasciatus*) and *brevis*, and (2) a southern group consisting of *mitratus* and *elegans* (the placement of *reticulatus*, known only from a single specimen, in either group remains problematical until additional material can be studied). On the basis of the similar heterogeneous scalation,

juvenile color pattern, and many skeletal features (Kluge, 1962), the southern group of species appears to be more closely related to the present-day *Eublepharis* (particularly *macularius* and *hardwickii*) than do any of the species of the northern group which are considerably closer geographically to the proposed route of entry into the New World. The southern group occurs in what is believed to be a derivative of the ancestral tropical flora of the New World in which the genus evolved. The much more highly evolved northern group of species occupies primarily the North American deserts which geologically and floristically have had a relatively recent and varied evolution (Axelrod, 1958). These facts may explain the marked differences between the two species groups in morphologic divergence from the primitive form and the degree of subspecific differentiation (Klauber, 1945).

An interesting point arises from a consideration of the development of the desert habitat preference of the northern species group in *Coleonyx* and of the Old World genera that belong to the subfamily. The Sonora, Mojave, Chihuahua, and other associated deserts arose during the expansion of a regional dry climate following the Eocene (Axelrod, 1960). With most of the deserts of the Old World, the Sahara, Pakistan, and Indian, also developing at this time, it must be assumed that multiple parallelism in habitat preference evolved in all the genera of the Eublepharinae, with the exception of the primitive forest type, *Aeluroscalabotes*. It appears that the ancestral stock of the northern species group of *Coleonyx* was present in the pre-desert habitat and, as deserts became available, the various groups as we know them today moved into arid regions (Axelrod, 1950). The occurrence of some of the more primitive forms of the northern species group (*C. variegatus abboti* and *C. v. peninsularis*; Klauber, 1945) in chaparral and subtropical scrub may be indicative of the pre-desert habitat of the ancestral stock of the northern group (Savage, 1960).

The two African genera (*Holodactylus* and *Hemitheconyx*) are morphologically very different from each other and probably did not evolve *in situ* from an ancestral form by simple geographical splitting. The magnitude of

the morphological differences seems to suggest two independent and temporally well-spaced lines of evolution from the wide-ranging *Eublepharis* ancestor of southern Asia. This thesis is best exemplified by the distribution of the supratemporal among the three genera: present in *Holodactylus* and *Eublepharis macularius* and *E. kuroiwaie orientalis*, absent from *Hemitheconyx* and *E. hardwickii*. The absence of the Eublepharinae from the more arid parts of southern Africa today may be due to replacement by the major gekkonine radiation that centered in that region (Loveridge, 1947). Another explanation might be that both African eublepharine genera evolved in the xeric environment of the lower-middle latitude of the Northern Hemisphere (map 1), which began to develop in the early Tertiary, and that they have been unable to cross the more mesic equatorial tropics into the Southern Hemisphere.

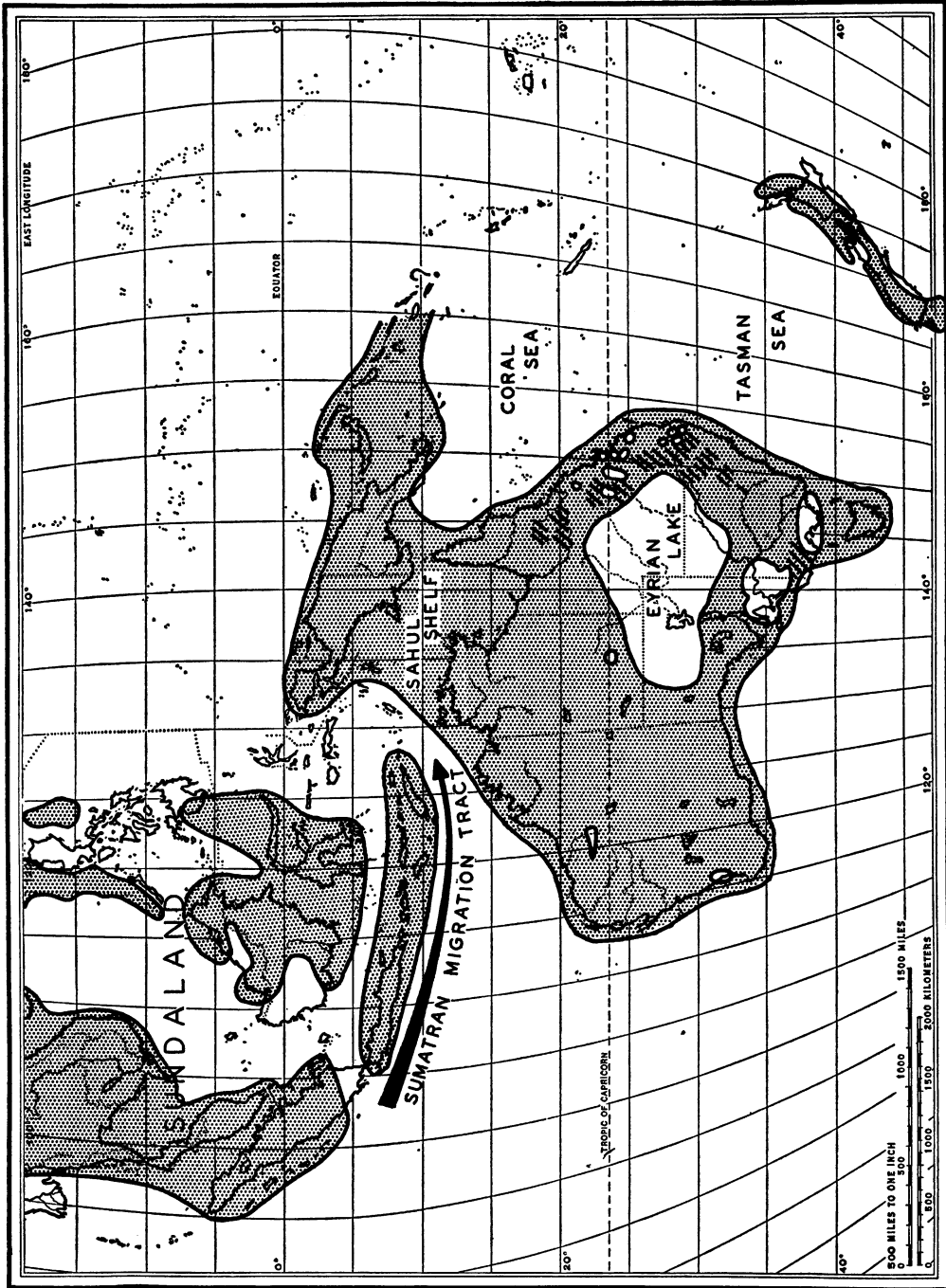
The theory of continental drift is not considered germane to a discussion of the zoogeography of the Gekkonidae, particularly the Diplodactylinae. Fairbridge (1953) has shown in his studies on the Sahul Shelf (map 2) that the Wegenerian hypothesis of the drifting northward of Australia during the Mesozoic and Tertiary is geologically untenable. Glaessner (1962) stated that New Guinea has maintained its position relative to Australia since the Jurassic. On the basis of faunal and floral evidence, Irving (1958), Burbidge (1960), Fleming (1962), and others have cast considerable doubt on the possibility of continental movement in the Australian Region during the Mesozoic and Tertiary.

It appears that the Diplodactylinae evolved from the primitive gekkonid stock in the tropics of southeast Asia some time during the late Mesozoic. The modern Diplodactylinae are restricted to the Australian Region (Australia, New Caledonia, Loyalty Islands, and New Zealand; see map 1) and do not appear to have radiated outside this biogeographic area (Darlington, 1957). It appears that the ancestral diplodactyline stock, following its probable origin in southeast Asia from a eublepharine ancestor, dispersed in the direction of Australia through the general region of the Indo-Australian archipel-

ago (map 2). Glaessner (1962) postulated that during the Upper Cretaceous (more precisely at the end of the Maestrichtian stage) a "wide-open" land connection existed between Australia and southeast Asia. He stated that extensive, long-term, land connections between these two areas existed only at the end of the Cretaceous. If the Diplodactylinae migrated toward Australia over this particular land bridge at this time, it follows that the subfamily must have originated in southeast Asia at an earlier time in the Mesozoic. This thesis is in accord with the time and place postulated for the evolution of the family. It is important to note that the Upper Cretaceous has also been recognized as the epoch in which the proto-Australian marsupial stock migrated into the region by way of the Indo-Australian land bridge (David, 1950; Glaessner, 1962; Simpson, 1961).

It is generally accepted that following the Mesozoic, during the Paleocene (map 2), the sea inundated the land, and a major water barrier was formed between southeast Asia and Australia (Termier and Termier, 1952). It has been suggested by Burbidge (1960) that floral and faunal migrational advances from southeast Asia to Australia over this water barrier might have been permitted in the early Tertiary by way of "insular stepping stones." The Sahul Shelf (map 2) may have been exposed completely or in part at different times during this period, and it seems likely that it would at least have reduced the effect of the ocean as a barrier to migration. The possibility that the diplodactyline ancestor migrated to the Australian Region during the early Tertiary by "island hopping," as Simpson (1961) proposed for marsupials, should not be totally discounted in view of the well-known rafting abilities of modern gekkonines (McCann, 1953, 1955; Brown and Alcalá, 1957). This time is, however, somewhat in conflict with the early and middle Tertiary periods postulated for the evolution and dispersal of the subfamily (see previous discussion, and Kluge, MS).

The proposed route by which the diplodactyline ancestor moved into the region of Australia coincides with the Sumatran Migration Tract postulated by van Steenis (1934a, 1934b, 1936) on the basis of his



MAP. 2. Probable form of the exposed land mass (stippled) of southeast Asia, Australia (and New Guinea), and New Zealand during the Paleocene (modified after David, 1950; Termier and Termier, 1952; Fleming, 1962). The Sumatran Migration Tract of van Steenis and the Sahul Shelf are indicated. The early Tertiary Eyrrian Lake and eastern Australian lake system and basaltic flows (diagonal lines) are shown on the Australian continent. The Paleotropical-Tertiary Geoflora is believed to have covered all of the exposed land surfaces, with the possible exception of the southern part of Tasmania and New Zealand.

studies on the primitive, tropical, montane Malaysian flora (map 2). David (1950), considering isolation and all related events, hypothesized that the autochthonous Australian fauna developed during the Tertiary. The Diplodactylinae are believed to be a prime example of the autochthonous fauna of this region.

By Upper Eocene time and continuing on into the Pliocene the sea surrounded Australia and covered most of New Guinea with the exception of its southernmost part (David, 1950; Glaessner, 1962). The West-Australian (and associated Timor-East Celebes), Tasman, and Papuan geosynclines appear to have formed the major seaways isolating this region during the Tertiary. It is postulated that the diplodactyline stock was resident in the Australian Region (inclusive of Australia and New Guinea) by at least Paleocene-Eocene time (map 2).

Concurrent, or nearly so, with the origin of the Diplodactylinae from a southeast Asian eublepharine ancestor and movement in the direction of the Indo-Australian archipelago, the Gekkoninae probably dispersed westward through southwestern Asia toward Africa. There is a moderately large number of gekkonine genera in Africa and Madagascar and in southwestern Asia that exhibit a few morphological similarities, such as fused nasals and paired frontals (see individual discussions of subfamilial diagnostic characters), and appear to be relatively closely related. *Teratoscincus* (and possibly *Stenodactylus*) almost certainly formed another evolutionary line on the basis of the increased ossicle number and presence of an angular in the lower jaw. Possibly these groups of genera represent concentrated remnants of the earliest gekkonine radiations. The Oriental, Oceanic, and Australian regions support only "modern expanding dominants" (Underwood, 1957), such as *Gehyra*, *Cyrtodactylus*, *Lepidodactylus*, and *Gekko*, and more primitive forms do not appear to have evolved in the eastern Paleotropical areas.

On the basis of their extreme morphological differences, the endemic gekkonine genera of the New World do not appear to form a natural group (Kluge, 1964). With few exceptions, each New World genus can be shown to be related to an Old World genus, or group

of genera, primarily African in distribution. As an indicator of relationships, Taylor and Leonard (1956) stressed the importance of the lack of preanal pores in all the endemic gekkonine genera of the New World. These authors apparently overlooked the fact that preanal pores are present in the genus *Briba* (Amaral, 1935). In any event, the erratic distribution of preanal pores in the Gekkoninae precludes the use of that character alone as an indicator of relationships. It seems likely that the New World gekkonine genera were in most cases independently derived from Old World ancestors. Occasional trans-Atlantic rafting for gekkos does not seem improbable in view of the favorable surface currents and winds (Darlington, 1957) and the time available for the formation of the rather limited New World fauna (McCann, 1953; Brown and Alcalá, 1957; King, 1962). The present distribution of *Tarentola* (one species in the West Indies and 10 species and subspecies in southern Europe and northern Africa, including the Canary Islands) is almost certainly a result of trans-Atlantic rafting. Late Pleistocene material of the species *T. americana* of the West Indies substantiates its presence in the New World before the arrival of European man (Etheridge, 1956b; also see Koopman and Ruibal, 1955). *Hemidactylus brooki* is very widely distributed in Africa and throughout the Greater Antilles and Colombia (= *H. leightoni*) in the New World. Its distribution in the New World does not appear to be associated with human activities, unlike that of the South American and Lesser Antillean *H. mabouia*. Another *Hemidactylus* species (undescribed) from northwestern South America and a *Lygodactylus* species (also undescribed) from Brazil may represent somewhat older, independent colonizations from their Old World congeners.

Superimposed both geographically and temporally on the earliest Old World gekkonine radiations are a large series of genera that I consider to be recent expanding dominants (e.g., *Gekko*, *Gehyra*, *Hemidactylus*, *Lepidodactylus*, *Cyrtodactylus*, and *Cnemaspis*). The degree of speciation, the distributional patterns, and the morphological specializations of these genera indicate their recent dominance and to some degree their

close relationship. There are still many gekkonine genera that do not appear to be representative of either the early or the more modern radiations. These genera are probably remnants of minor splinter groups that evolved for the most part from separate stocks of the earlier gekkonine radiations.

The Sphaerodactylinae are represented today by a morphologically and behaviorly well-circumscribed series of genera that are primarily restricted to the Neotropical Region (map 1). The ancestral sphaerodactyline doubtless was derived from a gekkonine stock (tables 2 and 3; fig 8), possibly near the African *Lygodactylus* and its relatives (*sensu lato*). This relationship is suggested primarily

on the basis of the common loss of cloacal sacs and bones and diurnal habits. It is possible that the ancestral sphaerodactyline stock arrived in the New World tropics at an early time (probably early Tertiary), by trans-Atlantic rafting. The strong African affinities certainly do not support a concept of a migration into the New World via the Bering land bridge. The dominance of the Sphaerodactylinae in the New World is possibly correlated with the absence of a major gekkonine radiation. The large number of species of *Sphaerodactylus* and *Gonatodes* demonstrates the success of the subfamily in this region.

SUMMARY

THE LIZARD FAMILY Gekkonidae consists of 82 genera and approximately 650 species. The family is found on the majority of land masses between latitude 50° N. and latitude 50° S. and has adapted to most environmental extremes therein. Important aspects of the general biology of these lizards are summarized for the first time. The relationships of the Gekkonidae to other modern lizards are briefly discussed, and the family is characterized in detail on the basis of internal and external morphology. It is suggested that the limbless lizards of the family Pygopodidae evolved directly from the Gekkonidae. The fossil history of gekkonoids is reviewed, and it appears that the extinct Upper Jurassic family Ardeosauridae is directly ancestral to gekkos. The Ardeosaurinae and the eublepharine gekkos have many characters in common. The Tertiary fossil gekkos *Rhodanogekko*, *Caudurcogekko*, and *Gerandogekko* appear to be more closely related to the Gekkoninae than to the other subfamilies as they are defined herein. These fossil genera and the Ardeosauridae are very similar to modern gekkos, which suggests an Upper Jurassic-Lower Cretaceous origin of the Gekkonidae.

The most recently proposed classification of gekkonid lizards, based on the shape of the pupil, does not appear to be a natural one because of the variability of the diagnostic character. A new subfamilial classification is proposed on the basis of an examination of the morphology of all 82 recognized genera, and 283 species and subspecies, represented by nearly 1000 specimens. The following characters are used in the diagnoses: (a) true eyelids or spectacle present, (b) premaxillary bone developing from one or two centers of ossification, (c) calcified postcranial endolymphatic sacs present or absent, (d) preanal organs or escutcheon scales present, (e) ability to vocalize present or absent, (f) number of eggs laid, two or one, (g) supratemporal bone present or absent, (h) number of scleral ossicles, (i) cloacal bones and sacs present or absent, (j) angular bone present or absent, (k) splenial bone present or absent, (l) frontal bone paired or single, (m) nasal bones paired or fused, (n) parietal bones paired or fused,

(o) presacral vertebrae procoelous or amphicoelous, (p) morphology of the hyoid arch, (q) morphology of the second visceral arch, and (r) squamosal bone present or absent. The number of character-states of each of the 18 diagnostic characters is discussed, and the primitive or advanced condition of each state and their numerical weights are given. Possible parallelisms are also indicated. On the basis of the greatest number of shared or unshared characters and least number of parallelisms, the 82 recognized genera are grouped into four subfamilies: the Eublepharinae, the Sphaerodactylinae, the Diplodactylinae, and the Gekkoninae. The last two subfamilies bear little resemblance to the taxa of the most recently proposed classification in terms of generic composition. The relationships of the four subfamilies are expressed in the form of a phyletic dendrogram which is superimposed on a background of advancement indexes (extrapolated from the numerical weighting of the character-states). The Diplodactylinae appear to have been derived directly from the most primitive subfamily, the Eublepharinae, whereas the Gekkoninae probably evolved from a considerably more advanced form. The gekkonid subfamily Sphaerodactylinae is the most advanced, and it appears to have been derived from the evolutionary stock that gave rise to the Gekkoninae. The four generic assemblages are considered to be of equal taxonomic rank (subfamilies), unlike that proposed in the most recent classification, because of the nearly uniform increase in the total advancement index from group to group.

The four taxonomic products are consistent with presently recognized zoogeographical concepts. It appears that southeastern Asia was the place of origin and early evolution of the circumglobal, now largely allopatric, Eublepharinae, and possibly all gekkonid lizards, some time during the Upper Jurassic-Lower Cretaceous. The eublepharine genus *Aeluroscalabotes* is restricted to this general region and appears to be the most primitive living genus of gekkos. *Eublepharis* is considered to be the closest living relative of *Aeluroscalabotes*. From the ancestral *Euble-*

pharis stock there appear to have been two separate lines of evolution within the subfamily: (1) a New World stock leading to *Coleonyx*, and (2) an African stock that gave rise to *Holodactylus* and *Hemitheconyx*. The magnitude of the morphological differences between the latter two genera may indicate that they did not evolve from a single ancestral *Eublepharis*-like population. The ancestor of *Coleonyx* probably arrived in the New World by way of the Bering land bridge through the continuous Paleocene Subtropical floral belt. The southern species group in *Coleonyx* (*elegans* and *mitratus*) appears to be more closely related to *Eublepharis* than is the northern group (*brevis* and *variegatus*). The occurrence of some populations of the northern group in chaparral and subtropical scrub is probably indicative of the pre-desert habitat preference of the complex.

The relatively primitive Diplodactylinae are restricted to the Australian Region (today, Australia, New Caledonia and the Loyalty Islands, and New Zealand). It seems likely that the ancestral diplodactyline stock, following its origin in southeast Asia from an eublepharine ancestor, dispersed in the direction of Australia through the general region of the Indo-Australian archipelago, probably during the late Mesozoic; the Diplodactylinae are considered a member of the autochthonous fauna of the Australian Region.

Concurrently, or nearly so, with the origin of the Diplodactylinae, it appears that the

Gekkoninae evolved and dispersed westward through southwestern Asia toward Africa. The Gekkoninae are clearly the dominant gekkos today in terms of speciation, diversity of biology, and distribution (continuous circumglobal distribution between approximately latitude 50° N. and latitude 50° S.). Within the Gekkoninae, there appear to have been at least three levels of evolution and radiation. At least two of the earlier gekkonine radiations seem to have centered in Africa and Madagascar and southwestern Asia. The eastern part of the Paleotropical area, in contrast to the west, is dominated by "modern expanding dominants" that belong primarily to the genera *Cyrtodactylus*, *Gehyra*, *Gekko*, and *Lepidodactylus*. The few endemic gekkonine genera of the New World do not appear to form a natural group and in most cases seem to have been independently derived from Old World ancestors, the majority of which have an African distribution today. Fortuitous trans-Atlantic rafting is postulated as the general way in which the ancestors of the gekkonine genera dispersed to the New World.

The Sphaerodactylinae are restricted to the New World (primarily the Neotropical Region) and may also have been derived from an African stock, possibly near the gekkonine genus *Lygodactylus* and its relatives. The dominance of the sphaerodactyline gekkos in the New World may be correlated with the absence of a single major gekkonine radiation from that part of its total range.

APPENDIX 1

ALL OSTEOLOGICAL DATA presented in this study were obtained from either cleared and stained specimens or skeletons cleaned by dermestid beetles of the following genera and species, unless otherwise stated in the text. The number of specimens used in the study follows the species name in parentheses. The shape of the pupil was studied in living material of those species marked with a subscript x. The species marked with an asterisk belong to the Museum of Comparative Zoology, Harvard University, osteological collection; the remaining material is in my personal collection.

Eublepharinae

- Aeluroscalabotes* Boulenger
d. dorsalis (2), *felinus** (1)
Coleonyx Gray
brevis (15), *e. elegans* (4), *mitratus* (2),
variegatus (including *v. variegatus* and *v. sonoriensis*) (47)_x
Eublepharis Gray
hardwickii (1), *macularius* (3)
Hemitheconyx Stejneger
*caudicinctus** (1)
Holodactylus Boettger
*africanus** (1)

Diplodactylinae

- Bavayia* Roux
cyclura (1)
Carphodactylus Günther
laevis (1)_x
Crenadactylus Dixon and Kluge
ocellatus (8)_x
Diplodactylus Gray
alboguttatus (1), *byrnei* (1), *c. ciliaris* (4)_x, *c. intermedius* (10)_x, *conspicillatus* (2)_x, *damaeus* (7)_x, *elderi* (1)_x, *maini* (2)_x, *michaelseni* (1), *pulcher* (6)_x, *savagei* (1), *spinigerus* (5)_x, *squarrosus* (1)_x, *steindachneri* (1), *steno-*
dactylus (8)_x, *strophurus* (2), *taenicauda* (4)_x, *tessellatus* (3), *vittatus* (14)_x, *williamsi* (5)_x
Heteropholis Fischer
tuberculatus (1)
Hoplodactylus Fitzinger
duvaucelii (3), *granulatus* (4), *pacificus* (3)
Nautilinus Gray
elegans (2)_x
Nephrurus Günther
asper (2), *laevissimus* (1)_x, *l. levis* (5)_x, *w. wheeleri* (1)

- Oedura* Gray
l. lesueurii (3)_x, *marmorata* (1), *monilis* (1)_x,
robusta (1), *tryoni* (1)_x
Phyllurus Schinz
cornutus (2)_x, *milii* (11)_x, *platurus* (3)_x,
sphyrurus (1)
Pseudothecadactylus Brongersma
australis (1)
Rhacodactylus Fitzinger
auriculatus (1)
Rhynchoedura Günther
ornata (5)_x
Gekkoninae
Afroedura Loveridge
p. pondolia (1), *transvaalica platyceps* (1)
Agamura Blanford
persica (1)
Ailuronyx Fitzinger
seychellensis (1)
Aristelliger Cope
cochranae barbouri (2), *p. praesignis* (4)_x
Blaesodactylus Boettger
boivini (1)
Briba Amaral
brasiliana (1)
Bunopus Blanford
tuberculatus (1)
Calodactylodes Strand
aureus (1)
Chondrodactylus Peters
angulifer (1)
Cnemaspis Strauch
boulengerii (1), *kandiana* (1), *kendallii* (1),
q. quattuorseriata (1), *wynadensis* (1)
Colopus Peters
wahlbergii (1)
Cosymbotus Fitzinger
platyurus (1)_x
Crossobamon Boettger
maynardi (1), *orientalis* (2)
Cyrtodactylus Gray
annulatus (1), *kachhensis watsoni* (1), *louis-*
adensis (1), *marmoratus* (1), *nebulosus* (1),
p. pelagicus (1)_x, *scaber* (1)
Ebenavia Boettger
inunguis (1)
Geckolepis Grandidier
maculata (1)
Geckonia Mocquard
chazaliae (1)
Gehyra Gray
australis (2)_x, *mutilata* (11)_x, *oceanica* (2),
punctata (14)_x, *variegata* (16)_x
Gekko Laurenti
g. gecko (6)_x, *vittatus* (2)

- Gymnodactylus* Spix
g. geckoides (1)
- Hemidactylus* Oken
b. brooki (2)_x, *b. angulatus* (1), *b. haitianus* (5), *flaviviridis* (1), *frenatus* (13)_x, *garnotii* (1), *giganteus* (1), *karenorum* (5), *leschenaultii* (1), *maculatus* (1), *persicus* (1), *t. turcicus* (2)_x
- Hemiphyllodactylus* Bleeker
t. typus (3)
- Heteronotia* Wermuth
binoei (11)_x, *spelea* (1)
- Homonota* Gray
darwinii (2), *gaudichaudii* (3), *horrida* (7)
- Homopholis* Boulenger
fasciata subsp. (1), *wahlbergii* (1)
- Lepidodactylus* Fitzinger
guppyi (1), *lugubris* (13)_x, *pumilis* (2), *woodfordi* (1)
- Lygodactylus* Gray
capensis (2), *conraui* (1), *p. picturatus* (1)
- Microgecko* Nikol'sky
helenae (2)
- Milloisaurus* Pasteur
mirabilis (1)
- Narudasia* Methuen and Hewitt
festiva (1)
- Pachydactylus* Wiegmann
b. bibronii (7)_x, *b. turneri* (1), *c. capensis* (1), *geitje* (1)
- Palmatogecko* Anderson
rangei (2)
- Perochirus* Boulenger
guentheri (2)
- Phelsuma* Gray
barbouri (1)_x, *cepediana* (2), *laticauda* (2)_x, *lineata* subsp. (1), *m. madagascariensis* (1)_x, *m. kochi* (1)_x
- Phyllodactylus* Gray
guentheri (1), *h. homolepidurus* (2)_x, *julieni* (1), *lanei* subsp. (1), *marmoratus* (11)_x, *p. porphyreus* (1), *t. tuberculatus* (2)_x, *unctus* (1)_x, *xanti nocticolus* (1)
- Phyllopezus* Peters
p. pollicaris (1), *p. przewalskii* (2)
- Pristurus* Rüppell
carteri collaris (1), *crucifer* (2), *f. flavipunctatus* (3), *sokotranus* (1)
- Ptenopus* Gray
garrulus (1)
- Ptychozoon* Kuhl
kuhli (1)
- Ptyodactylus* Goldfuss
h. hasselquistii (1), *h. ourdii* (1)
- Quedenfeldtia* Boettger
trachyblepharus (4)
- Rhoptropella* Hewitt
ocellata (1)
- Rhoptropus* Peters
afer (1), *b. bradfieldi* (1)
- Saurodactylus* Fitzinger
fasciatus (2), *mauritanicus brosetti* (4)
- Stenodactylus* Fitzinger
petrii (1), *s. sthenodactylus* (6), *s. mauritanicus* (1)
- Tarentola* Gray
americana (1), *annularis* (1), *m. mauritanica* (5)_x, *neglecta* (1)
- Teratolepis* Günther
albofasciata (3), *fasciata* (7)
- Teratoscincus* Strauch
microlepis (4)_x, *scincus* (5)_x
- Thecadactylus* Goldfuss
rapicauda (2)
- Tropicolotes* Peters
tripolitanus algericus (1)
- Uroplatus* Duméril
f. fimbriatus (1)
- Sphaerodactylinae
- Coleodactylus* Parker
amazonicus (2)
- Gonatodes* Fitzinger
a. albogularis (2), *a. fuscus* (3)_x, *a. notatus* (1), *antillensis* (3), *atricucularis* (3), *humeralis* (2), *ocellatus* (1), *v. vittatus* (2)
- Lepidoblepharis* Peracca
microlepis (2)_x
- Pseudogonatodes* Ruthven
barbouri (2)
- Sphaerodactylus* Wagler
argus henriquesi (3), *cinereus* (2), *difficilis* (2), *goniorhynchus* (2), *inaguae* (2), *m. macrolepis* (2), *mariguanae* (1), *merlensi* (1), *parkeri* (2), *richardsonii gossei* (1), *torrei* (1)

LITERATURE CITED

- AMARAL, AFRANIO DO
 1935. Estudos sobre lacertilio Neotropicos. III Um novo genero e duas novas especies de geckonideos e uma nova raça de amphisbenido, procedentes do Brasil Central. Mem. Inst. Butantan, vol. 9, pp. 253-256.
- ANDERSON, JOHN
 1896. A contribution to the herpetology of Arabia, with a preliminary list of the reptiles and batrachians of Egypt. London, Taylor and Francis, pp. 1-122.
- ANNANDALE, N.
 1905. Notes on some Oriental geckos in the Indian Museum, Calcutta, with descriptions of new forms. Ann. Mag. Nat. Hist., ser. 7, vol. 15, art. 3, pp. 26-32.
- AXELROD, DANIEL I.
 1950. Evolution of desert vegetation in western North America. Publ. Carnegie Inst. Washington, Contrib. Paleont., no. 590, pp. 215-306.
 1952. A theory of angiosperm evolution. Evolution, vol. 6, no. 1, pp. 29-60.
 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev., vol. 24, no. 7, pp. 433-509.
 1959. Poleward migration of the early angiosperm flora. Science, vol. 130, no. 3369, pp. 203-207.
 1960. The evolution of flowering plants. In Tax, Sol (ed.), The evolution of life. Chicago, University of Chicago Press, pp. 227-305.
- BAIRD, DONALD
 1964. *Changisaurus* reinterpreted as a Jurassic turtle. Jour. Paleont., vol. 38, no. 1, pp. 126-127.
- BELLAIRS, A. D'A.
 1948. The eyelids and spectacle in geckos. Proc. Zool. Soc. London, vol. 118, pp. 420-425.
- BONS, J.
 1959. Les lacertiliens du Sud-ouest Marocain. Trav. l'Inst. Sci. Chérifien, Rabat, Zool., no. 18, pp. 1-130.
- BOULENGER, GEORGE A.
 1885. Catalogue of the lizards in the British Museum (Natural History). Second edition. London, Taylor and Francis, vol. 1, pp. 1-436.
- BRAIN, C. K.
 1962a. A review of the gecko genus *Ptenopus* with the description of a new species. Cimbebasia, no. 1, pp. 1-18.
 1962b. Observations on the temperature tolerance of lizards in the central Namib desert, South West Africa. *Ibid.*, no. 4, pp. 1-5.
- BRATTSTROM, B. H.
 1965. Body temperatures of reptiles. Amer. Midland Nat., vol. 73, no. 2, pp. 376-422.
- BRONGERSMA, L. D.
 1934. Contributions to Indo-Australian herpetology. Leiden, E. J. Brill, pp. 1-251.
- BROWN, W. C., AND A. G. ALCALA
 1957. Viability of lizard eggs exposed to sea water. Copeia, no. 1, pp. 39-41.
- BURBIDGE, NANCY T.
 1960. The phytogeography of the Australian Region. Australian Jour. Bot., vol. 8, no. 2, pp. 75-212.
- BUSTARD, H. R.
 1963. Gecko behavioral trait: tongue wiping spectacle. Herpetologica, vol. 19, no. 3, pp. 217-218.
 1964. Defensive behavior shown by Australian geckos, genus *Diplodactylus*. *Ibid.*, vol. 20, no. 3, pp. 198-200.
- CAGLE, F. R.
 1946. A lizard population on Tinian. Copeia, no. 1, pp. 4-9.
- CAMP, CHARLES L.
 1923. Classification of the lizards. Bull. Amer. Mus. Nat. Hist., vol. 48, art. 11, pp. 289-481.
- CHURCH, GILBERT
 1962. The reproductive cycles of the Javanese house geckos, *Cosymbotus platyurus*, *Hemidactylus frenatus*, and *Peropus mutilatus*. Copeia, no. 2, pp. 262-269.
- COGGER, HAROLD G.
 1964. The comparative osteology and systematic status of the gekkonid genera *Afroedura* Loveridge and *Oedura* Gray. Proc. Linnean Soc. New South Wales, vol. 89, pt. 3, pp. 364-372.
- COLE, CHARLES J.
 1966. Femoral glands of the lizard, *Crotaphytus collaris*. Jour. Morph., vol. 118, no. 1, pp. 119-135.
- COPE, EDWARD D.
 1868. Observations on reptiles of the Old World. Art. II. Proc. Acad. Nat. Sci. Philadelphia, no. 5, pp. 316-323.
- DARLINGTON, PHILIP J., JR.
 1957. Zoogeography: The geographical dis-

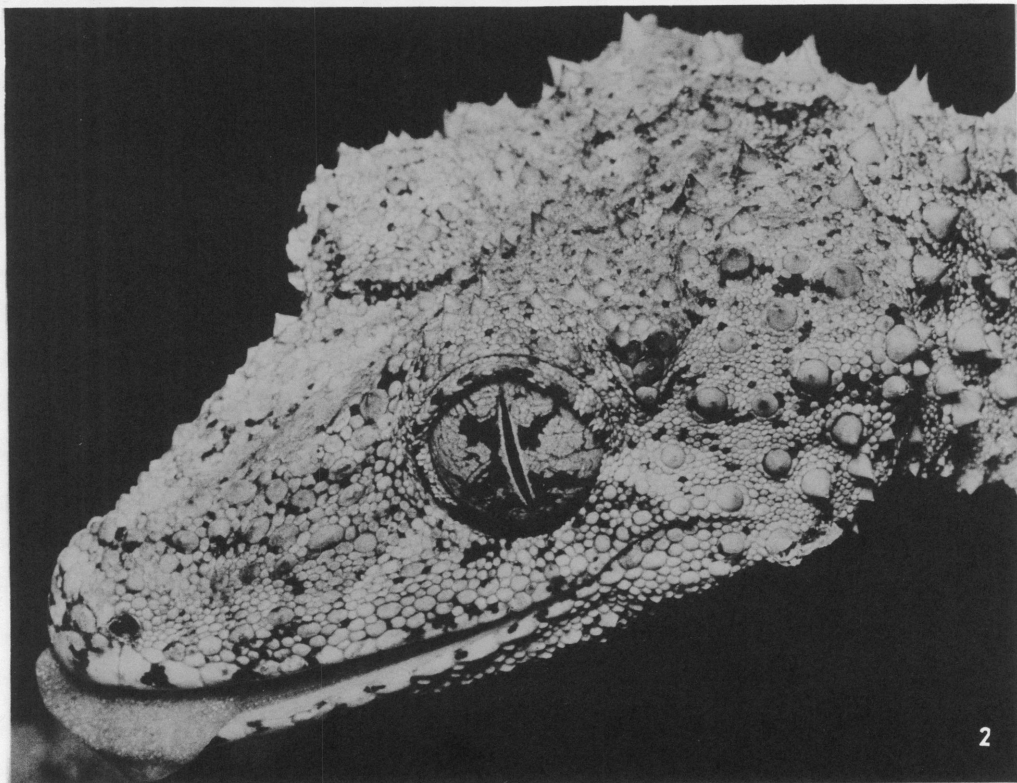
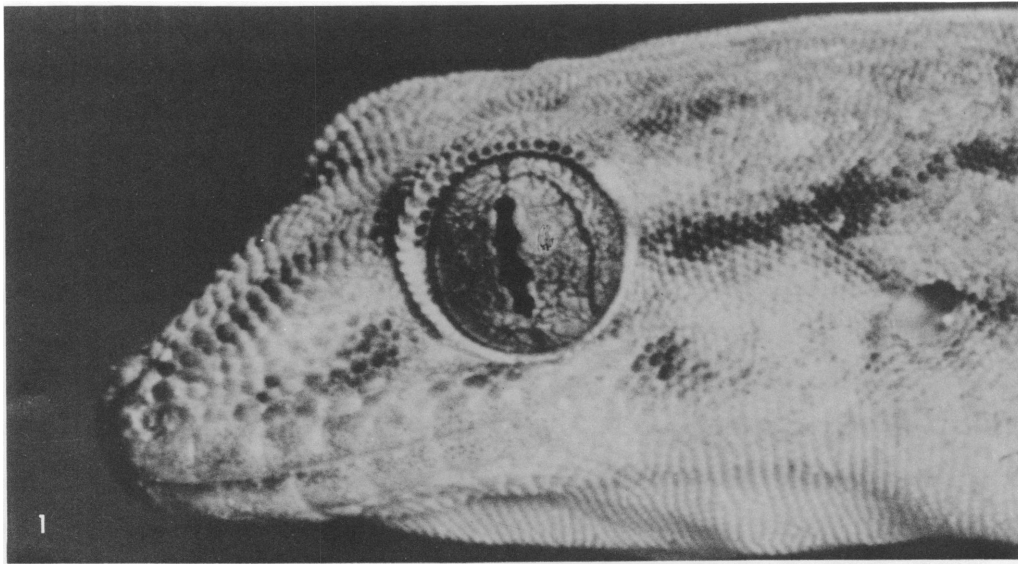
- tribution of animals. New York, John Wiley and Sons, pp. 1-675.
- DAVID, T. W. EDGEWORTH
1950. The geology of the Commonwealth of Australia. London, Edward Arnold and Co., vol. 1, pp. 1-747.
- DAVIS, D. DWIGHT, AND U. R. GORE
1947. Clearing and staining skeletons of small vertebrates. *Fieldiana, Technique*, no. 4, pp. 1-16.
- DE BEER, G. R.
1937. The development of the vertebrate skull. London, Oxford University Press, pp. 1-552.
- DENTON, E. J.
1956. The response of the pupil of *Gekko gekko* to external light stimulus. *Jour. Gen. Physiol.*, vol. 40, no. 2, pp. 201-216.
- EDINGER, TILLY
1929. Über knöcherne Scleralringe. *Zool. Jahr. Abt. f. Anat.*, vol. 51, pt. 2, pp. 163-226.
- ESTES, RICHARD
1963. Early Miocene salamanders and lizards from Florida. *Quart. Jour. Florida Acad. Sci.*, vol. 26, no. 8, pp. 234-256.
- ETHERIDGE, RICHARD
1964. Late Pleistocene lizards from Barbuda, British West Indies. *Bull. Florida State Mus., Biol. Sci.*, vol. 9, no. 2, pp. 43-75.
1965a. Fossil lizards from the Dominican Republic. *Quart. Jour. Florida Acad. Sci.*, vol. 28, no. 1, pp. 83-105.
1965b. Pleistocene lizards from New Providence. *Ibid.*, vol. 28, no. 4, pp. 349-358.
[MS.] The relationships of the anoles (Reptilia: Sauria: Iguanidae); an interpretation based on skeletal morphology. Ann Arbor, University of Michigan, unpublished doctoral dissertation, 1959, pp. 1-236.
- FAIRBRIDGE, R. W.
1953. The Sahul Shelf, northern Australia, its structure and geological relationships. *Jour. Roy. Soc. Western Australia*, vol. 37, pt. 1, pp. 1-33.
- FÉLIZET, J.
1911. Recherches sur les glandes femorales de *Lacerta muralis*. *Jour. d'Anat. Physiol.*, vol. 47, pp. 333-370.
- FLEMING, CHARLES A.
1962. New Zealand biogeography, a paleontologist's approach. *Tuatara*, vol. 10, pt. 2, pp. 53-108.
- GADOW, HANS
1901. Amphibia and reptiles. *In Cambridge natural history*. London, vol. 8, pp. 1-668.
- GIEBEL, C.
1862. Wirbelthier und Insektenreste im Bernsteln. *Zeitschr. Ges. Naturwiss. Berlin*, vol. 20, no. 10, pp. 311-321.
- GLAESSNER, M. F.
1962. Isolation and communication in the geological history of the Australian fauna. *In* Leeper, G. W. (ed.), *The evolution of living organisms*. Melbourne, Melbourne University Press, pp. 242-249.
- GOIN, C. J., AND O. B. GOIN
1962. Introduction to herpetology. San Francisco, W. H. Freeman and Co., pp. 1-341.
- GREENBERG, B.
1943. Social behavior of the western banded gecko, *Coleonyx variegatus* Baird. *Physiol. Zool.*, vol. 16, no. 1, pp. 110-122.
- GUGG, WOLFGANG
1939. Der Skleralring der plagiötremen Reptilien. *Zool. Jahr. Abt. f. Anat.*, vol. 65, pt. 3, pp. 339-416.
- HAACKE, W. D.
1964. Description of two new species of lizards and notes on *Fitzsimonsia brevipes* (FitzSimons) from the central Namib desert. *Sci. Papers Namib Des. Res. Sta.*, no. 25, pp. 1-15.
- HAAS, GEORG
1957. Some amphibians and reptiles from Arabia. *Proc. California Acad. Sci.*, vol. 29, no. 3, pp. 47-86.
- HARDIN, JAMES W.
1957. A revision of the American Hippocastanaceae. *Brittonia*, vol. 9, no. 3, pp. 145-171.
- HECHT, MAX K.
1951. Fossil lizards of the West Indian genus *Aristelliger* (Gekkonidae). *Amer. Mus. Novitates*, no. 1538, pp. 1-33.
- HOFFSTETTER, ROBERT
1946. Sur les Gekkonidae fossiles. *Bull. Mus. Natl. d'Hist. Nat., Paris*, ser. 2, vol. 18, no. 2, pp. 195-203.
1961. Le gisement de vertébrés Miocènes de Beni Mellal (Maroc). *Squamates. Notes Mém. Serv. Mines Carte Géol. Maroc*, Rabat, no. 155, pp. 95-101.
1962. Problemes actuels de paléontologie (évolution des vertébrés). *Colloq. Internatl. Centre Natl. Rech. Sci., Paris*, no. 104, pp. 243-279.
1964. Les Sauria du Jurassique supérieur et spécialement les Gekkota de Bavière et de Mandchourie. *Senckenbergiana Biol.*, vol. 45, no. 3/5, pp. 281-324.

- HOLDER, LYNETTE A.
1960. The comparative morphology of the axial skeleton in the Australian Gekkonidae. *Jour. Linnean Soc. London, Zool.*, vol. 44, no. 297, pp. 300-335.
- HOOFIEN, J. H.
1962. An unusual congregation of the gekkonid lizard *Tarentola annularis* (Geoffroy). *Herpetologica*, vol. 18, no. 1, pp. 54-56.
- INGER, R. F., AND W. KING
1961. A new cave-dwelling lizard of the genus *Cyrtodactylus*. *Sarawak Mus. Jour.*, vol. 18, nos. 17-18 (new ser.), pp. 274-276.
- IRVING, E.
1958. Rock magnetism: a new approach to the problems of polar wandering and continental drift. *Univ. Tasmania Geol. Dept. Symposium*, 1956, pp. 24-61.
- KÄSTLE, W.
1962. Kalk als Zusatznahrung für Echsen. *Aquar. Terrar. Zeitschr.*, vol. 15, p. 62.
- KING, WAYNE
1962. The occurrence of rafts for dispersal of land animals into the West Indies. *Quart. Jour. Florida Acad. Sci.*, vol. 25, no. 1, pp. 45-52.
- KLAUBER, LAURENCE M.
1945. The geckos of the genus *Coleonyx* with descriptions of new subspecies. *Trans. San Diego Soc. Nat. Hist.*, vol. 10, no. 11, pp. 133-216.
- KLUGE, ARNOLD G.
1962. Comparative osteology of the eublepharid lizard genus *Coleonyx* Gray. *Jour. Morph.*, vol. 110, no. 3, pp. 299-332.
1963. A review of the gekkonid lizard genus *Heteronota* Gray, with a description of a new species from Western Australia. *Jour. Roy. Soc. Western Australia*, vol. 46, pt. 2, pp. 63-67.
1964. A revision of the South American gekkonid lizard genus *Homonota* Gray. *Amer. Mus. Novitates*, no. 2193, pp. 1-41.
[MS.] The Australian gekkonid lizard genus *Diplodactylus* Gray: an evolutionary and zoogeographical study. Los Angeles, University of Southern California, unpublished doctoral dissertation, 1965, pp. 1-472.
- KOOPMAN, K. F., AND R. RUIBAL
1955. Cave-fossil vertebrates from Camaguey, Cuba. *Breviora*, no. 46, pp. 1-8.
- KOPSTEIN, FELIX
1938. Ein Beitrag zur Eierkunde und zur Fortpflanzung der Malaiischen Reptilien. *Bull. Raffles Mus.*, no. 14, pp. 81-167.
- LELLINGER, DAVID B.
[MS.] A quantitative study of generic delimitation in the adiantoid ferns. Ann Arbor, University of Michigan, unpublished doctoral dissertation, 1965, pp. 1-259.
- LOVERIDGE, ARTHUR
1947. Revision of the African lizards of the family Gekkonidae. *Bull. Mus. Comp. Zool.*, vol. 98, no. 1, pp. 1-469.
- MCCANN, CHARLES
1953. Distribution of the Gekkonidae in the Pacific area. *Proc. Seventh Pacific Sci. Congr. (Zool.)*, vol. 4, pp. 27-32.
1955. The lizards of New Zealand, Gekkonidae and Scincidae. *Dominion Mus. Bull.*, no. 17, pp. 1-127.
- MADERSON, P. F. A.
1964. Keratinized epidermal derivatives as an aid to climbing in gekkonid lizards. *Nature*, vol. 203, no. 4946, pp. 780-781.
- MANN, IDA
1931. Iris pattern in the vertebrates. *Trans. Zool. Soc. London*, vol. 21, pt. 4, no. 1, pp. 355-413.
- MAURER, F.
1896. Die ventrale Rumpfmuskulatur einiger Reptilien. Eine vergleichend-anatomische Untersuchung. *In Festschrift zum siebenzigsten Geburtstages von Carl Gegenbaur*. Leipzig, vol. 1, pp. 183-256.
1898. Die Entwicklung der ventralen Rumpfmuskulatur bei Reptilien. *Morph. Jahrb.*, vol. 26, pt. 1, pp. 1-60.
- MELL, R.
1922. Beiträge zur Fauna sinica.—I. Die Vertebraten Südchinas; Feldlisten und Feldnoten der Säuger, Vögel, Reptilien, Batrachier. *Arch. f. Naturgesch.*, Berlin, vol. 88, sect. A, pt. 10, pp. 1-134.
- MERTENS, R.
1946. Die Warn- und Droh-Reaktionen der Reptilien. *Abhandl. Senckenbergische Naturf. Gesell.*, no. 471, pp. 1-108.
1955. Die Amphibien und Reptilien Südwestafrikas. Aus den Ergebnissen einer im Jahre 1952 ausgeführten Reise. *Ibid.*, no. 490, pp. 1-172.
- MITCHELL, FRANCIS J.
1965. Australian geckos assigned to the genus *Gehyra* Gray (Reptilia, Gekkonidae). *Senckenbergiana Biol.*, vol. 46, no. 4, pp. 287-319.
- NOBLE, GLADWYN K.
1921. The bony structure and phyletic relations of *Sphaerodactylus* and allied lacer-

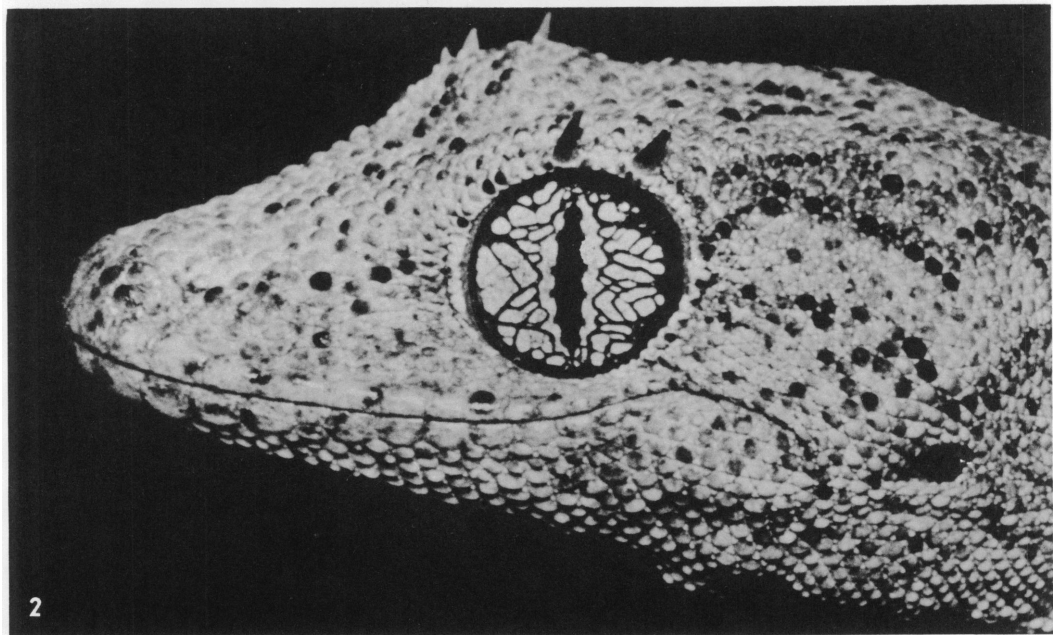
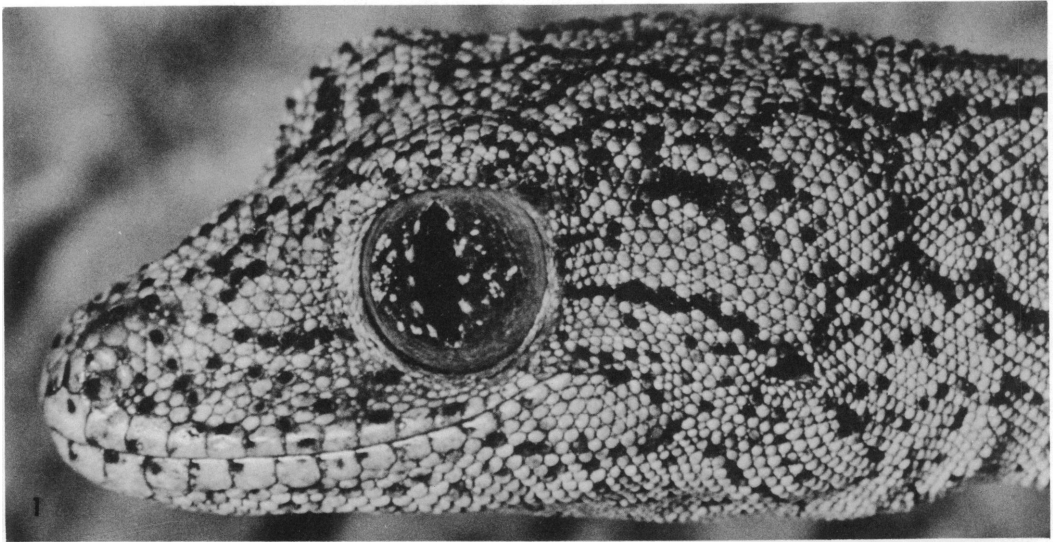
- tilian genera, with the description of a new genus. *Amer. Mus. Novitates*, no. 4, pp. 1-16.
- NOBLE, GLADWYN K., AND H. T. BRADLEY
1933. The mating behavior of lizards; its bearing on the theory of sexual selection. *Ann. New York Acad. Sci.*, vol. 35, art. 2, pp. 25-100.
- OLIVER, J. A., AND C. E. SHAW
1953. The amphibians and reptiles of the Hawaiian Islands. *Zoologica*, vol. 38, no. 2, pp. 65-95.
- PARKER, H. W.
1926. The Neotropical lizards of the genera *Lepidoblepharis*, *Pseudogonatodes*, *Lathrogecko*, and *Sphaerodactylus*, with the description of a new genus. *Ann. Mag. Nat. Hist.*, ser. 9, vol. 17, art. 41, pp. 291-301.
- PASTEUR, G.
1964. Recherches sur l'évolution des lygodactyles, lézards Afro-Malgaches actuels. *Trav. l'Inst. Sci. Chérifien*, Rabat, Zool., no. 29, pp. 1-132.
- PETERS, WILHELM C. H.
1865. Ueber einen im fossilen Copalharz eingeschlossen Gekko (*Hemidactylus*) aus Zanzibar. *Monatsber. Akad. Berlin*, pp. 455-457.
1866. A fossil lizard in Copal. *Ann. Mag. Nat. Hist.*, ser. 3, vol. 17, pp. 78-79.
- PIVETEAU, JEAN (ED.)
1955, 1966. *Traité de paléontologie*. Paris, Masson et C^{ie}, vols. 4, 5.
- POPE, CLIFFORD H.
1956. *The reptile world*. New York, Alfred A. Knopf, pp. 1-325.
- QUESNEL, V. C.
1957. The life history of the streak lizard, *Gonatodes vittatus* (Licht.). *Jour. Trinidad Field Nat. Club*, pp. 5-14.
- ROBINSON, PAMELA L.
1962. Gliding lizards from the Upper Keuper of Great Britain. *Proc. Geol. Soc. London*, no. 1601, pp. 137-146.
- ROMER, ALFRED S.
1956. *Osteology of the reptiles*. Chicago, University of Chicago Press, pp. 1-772.
- ROOIJ, NELLY DE
1915. The reptiles of the Indo-Australian Archipelago. Leiden, E. J. Brill, vol. 1, Lacertilia, Chelonia, Emydosauria, pp. 1-382.
- RUTH, EDWARD S.
1918. A study of the calcium glands in the common Philippine house lizard. *Philippine Jour. Sci. (B) Trop. Med.*, vol. 13, pp. 311-319.
- SAVAGE, JAY M.
1960. Evolution of a peninsular herpetofauna. *Syst. Zool.*, vol. 9, nos. 3-4, pp. 184-212.
- SCORA, RAINER W.
1966. The evolution of the genus *Monarda* (Labiatae). *Evolution*, vol. 20, no. 2, pp. 185-190.
- SIMPSON, G. G.
1953. *Evolution and geography*. The Condon Lectures. Eugene, Oregon State System of Higher Education, pp. 1-64.
1961. Historical zoogeography of Australian mammals. *Evolution*, vol. 15, no. 4, pp. 431-446.
- SLONAKER, J. R.
1918. A physiological study of the anatomy of the eye and its accessory parts of the English sparrow (*Passer domesticus*). *Jour. Morph.*, vol. 31, no. 3, pp. 351-459.
- SMITH, HOBART
1960. *Evolution of chordate structure*. New York, Holt, Rinehart and Winston, pp. 1-529.
- SMITH, MALCOLM A.
1933. Remarks on some Old World geckoes. *Rec. Indian Mus.*, vol. 35, pt. 1, pp. 9-19.
1935. The fauna of British India, including Ceylon and Burma. Reptilia and Amphibia. London, Taylor and Francis, vol. Sauria, pp. 1-440.
1939. Evolutionary changes in the eye coverings of certain lizards. *Proc. Linnean Soc. London*, 151st session, pp. 190-191.
- SPORNE, K. R.
1954. Statistics and the evolution of dicotyledons. *Evolution*, vol. 8, no. 1, pp. 55-64.
- STEBBINS, ROBERT C.
1961. Body temperature studies in South African lizards. *Koedoe*, no. 4, pp. 54-67.
- STEENIS, C. G. J. VAN
1934a. On the origin of the Malaysian mountain flora. 1. Facts and statement of problem. *Bull. Bot. Gardens Buitenzorg*, vol. 13, pp. 139-262.
1934b. On the origin of the Malaysian mountain flora. 2. Altitudinal zones, general considerations and renewed statement of the problem. *Ibid.*, vol. 13, pp. 289-417.
1936. On the origin of the Malaysian mountain flora. 3. Analysis of floristic relationships. Pt. 1. The Sumatran Track. *Ibid.*, vol. 14, pp. 56-72.
- STEPHENSON, N. G.
1960. The comparative osteology of Aus-

- tralian geckos and its bearing on their morphological status. *Jour. Linnean Soc. London, Zool.*, vol. 44, no. 297, pp. 278-299.
- STEPHENSON, N. G., AND ELSIE M. STEPHENSON
1956. The osteology of the New Zealand geckos and its bearing on their morphological status. *Trans. Roy. Soc. New Zealand*, vol. 84, pt. 2, pp. 341-358.
- STERZI, G.
1899. Die Rueckenmarkshüellen der schwanzlosen Amphibien. *Anat. Anz.*, vol. 16, no. 9, pp. 230-239.
- TAYLOR, EDWARD H.
1963. The lizards of Thailand. *Univ. Kansas Sci. Bull.*, vol. 44, no. 14, pp. 687-1077.
- TAYLOR, EDWARD H., AND A. BYRON LEONARD
1956. Concerning the relationships of certain Neotropical gekkonid genera, with comments on the microscopical structure of their glandular scales. *Ibid.*, vol. 38, pt. 1, no. 12, pp. 1019-1029.
- TERMIER, H., AND G. TERMIER
1952. *Histoire géologique de la biosphère*. Paris, Masson and C^{ie}, pp. 1-721.
- THROCKMORTON, L. H.
1965. Similarity versus relationship in *Drosophila*. *Syst. Zool.*, vol. 14, no. 3, pp. 221-236.
- UNDERWOOD, GARTH L.
1954. On the classification and evolution of geckos. *Proc. Zool. Soc. London*, vol. 124, pt. 3, pp. 469-492.
1955. Classification of geckos. *Nature*, vol. 175, p. 1089.
1957. On lizards of the family Pygopodidae. A contribution to the morphology and phylogeny of the Squamata. *Jour. Morph.*, vol. 100, no. 2, pp. 207-268.
1962. Reptiles of the eastern Caribbean. *Caribbean Affairs, Univ. West Indies, new ser.*, no. 1, pp. 1-192.
- VAILLANT, LÉON
1873. Sur un geckotien de l'ambre jaune. *Bull. Soc. Philom. Paris*, 1873 [July 26 meeting], pp. 65-67.
- WAGNER, WARREN H., JR.
1961. Problems in the classification of ferns. *In* Recent advances in botany (from lectures and symposia presented to the IX International Botanical Congress, Montreal 1959). Toronto, University of Toronto Press, vol. 1, pp. 841-844.
- WALLS, GORDON L.
1932. Pupil shapes in reptilian eyes. *Bull. Antivenin Inst. Amer.*, vol. 5, no. 3, art. 129, pp. 68-70.
1942. The vertebrate eye and its adaptive radiation. *Cranbrook Inst. Sci. Bull.*, no. 19, pp. 1-785.
- WERMUTH, HEINZ
1965. Liste der rezenten Amphibien und Reptilien: Gekkonidae, Pygopodidae, Xantusiidae. *In* *Das Tierreich*. Berlin, Lief. 80, pp. 1-246.
- WERNER, Y. L.
1956. Chromosome numbers of some male geckos (Reptilia: Gekkonidae). *Bull. Res. Council Israel*, vol. 5B, nos. 3-4, sect. 8, pp. 319-320.
1965. Über die israelischen Geckos der Gattung *Ptyodactylus* und ihre Biologie. *Salamandra*, vol. 1, nos. 1/2, pp. 15-25.
- WHITESIDE, BEATRICE
1922. The development of the *saccus endolymphaticus* in *Rana temporaria* Linné. *Amer. Jour. Anat.*, vol. 30, no. 2, pp. 231-266.
- WIEDERSHEIM, R.
1876. Zur Anatomie und Physiologie des *Phyllodactylus europaeus* mit besonderer Berücksichtigung des Aquaeductus vestibuli der Ascalaboten im Allgemeinen. *Morph. Jahrb.*, vol. 1, pt. 3, pp. 495-534.
- YOUNG, CHUNG-CHIEN
1959. On a new Lacertilia from Chingning, Chekiang, China. *Sci. Rec., Vert. Paleont.*, vol. 3, no. 10, pp. 520-523.

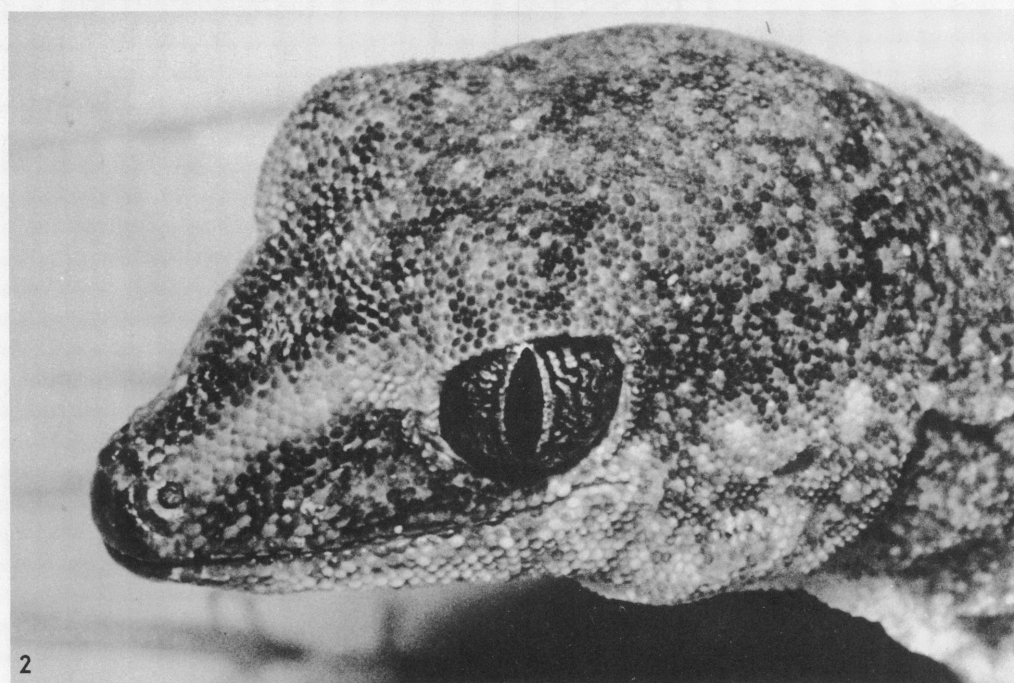
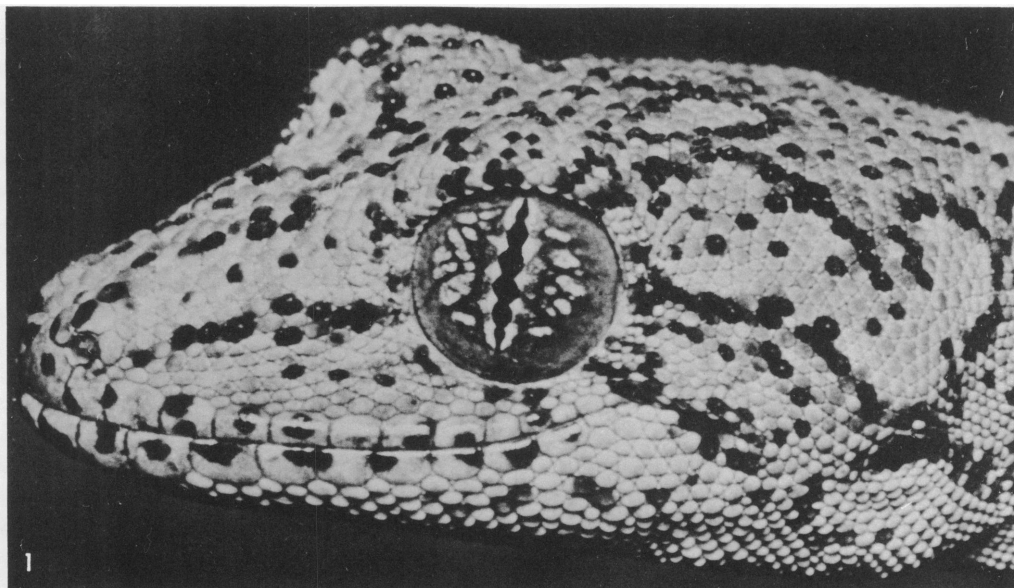
PLATES 1-5



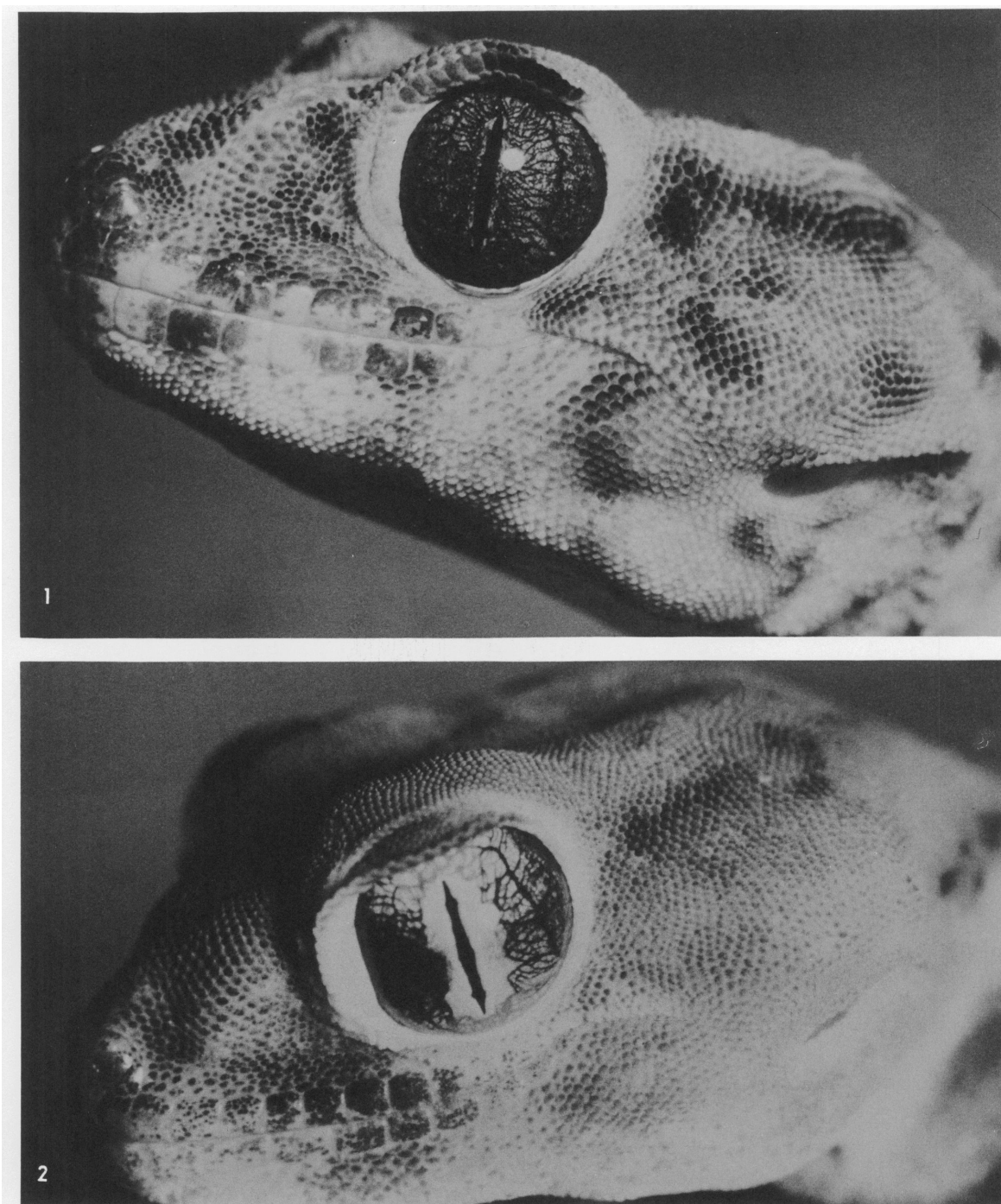
1. Shape of the gekkonine pupil; *Gehyra variegata*, from Lowood, Queensland, Australia. *Gehyra* was placed in the Gekkoninae by Underwood (1954). 2. Shape of the diplodactyline pupil; *Phyllurus cornutus*, from Mt. Tamborine, Queensland, Australia. *Phyllurus* was placed in the Diplodactylinae by Underwood (1954)



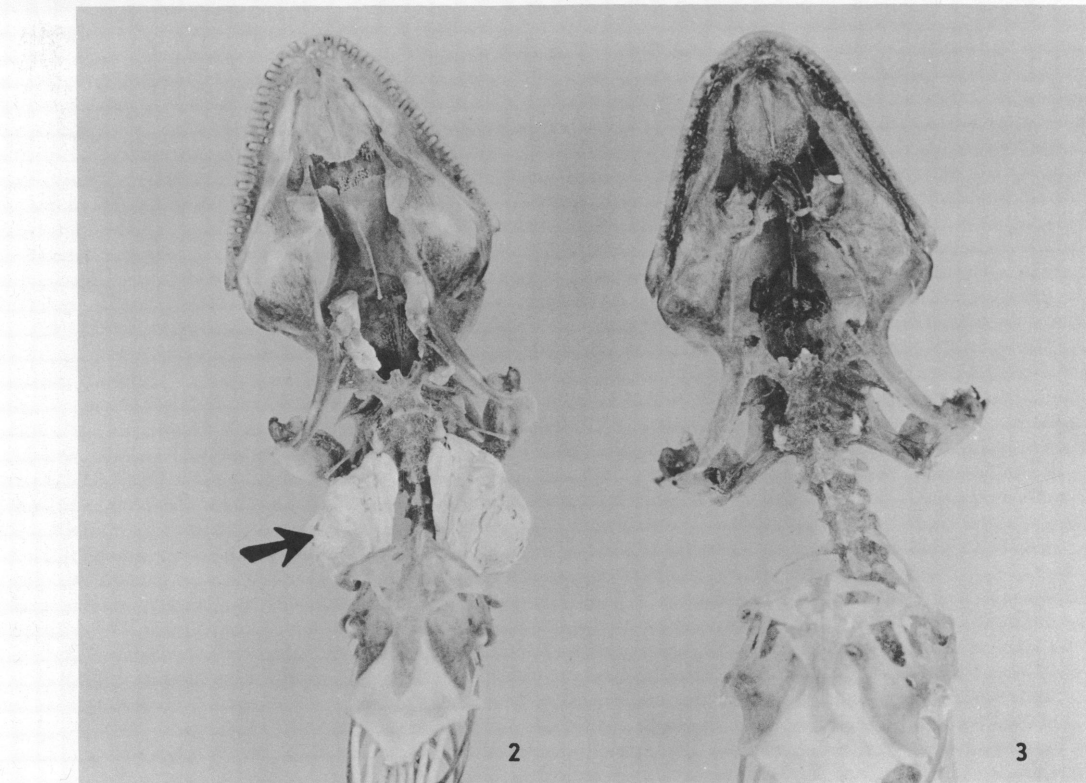
1, 2. Shapes of the gekkonine pupil. 1. *Diplodactylus williamsi* (emarginations poorly developed), from the Warrumbungle Mountains, New South Wales, Australia. 2. *Diplodactylus c. ciliaris*, from southern Queensland, Australia. *Diplodactylus* was placed in the Diplodactylinae by Underwood (1954)



1. Shape of the gekkonine pupil; *Diplodactylus ciliaris intermedius*, from Nymagee, New South Wales, Australia. 2. Shape of the diplodactyline pupil; *Diplodactylus conspicillatus*, from central Queensland, Australia



1, 2. Shapes of pupils intermediate between the gekkonine type and the diplodactyline type. 1. *Teratoscincus scincus*, from West Pakistan. 2. *Teratoscincus microlepis*, from West Pakistan. *Teratoscincus* was placed in the Diplodactylinae by Underwood (1954)



1. Shape of the diplodactyline pupil; *Nautilinus elegans*, from New Zealand. *Nautilinus* was placed in the Diplodactylinae by Underwood (1954). 2, 3. Ventral views of the cranium and thoracic regions of *Gekko g. gekko*, showing the calcified endolymphatic sacs (arrow). 2. Female, sac present. 3. Male, sac absent

